The significance of predation by soil invertebrates on field populations of *Agriolimax reticulatus* (Gastropoda, Limacidae).

by

MARGARET ELIZABETH TOD

Ph.D.

University of Edinburgh

1970.

SUMMARY

A serological technique was developed to enable slug tissues in gut contents to be identified with certainty, because preliminary feeding trials proved to be an unsatisfactory method for use in this type of study.

A trapping survey was made for one year to determine the seasonal distribution of possible predators in different habitats.

Gut contents were tested from the following beetles: Carabidae - 1,394 adults and 57 larvae; Staphylinidae - 94 adults; Silphidae - 15 adults and 3 larvae; Scarabaeidae - 2 adults; Cantharidae - one larva. 37 harvestmen (Phalangida), one earwig (Dermaptera) and 19 centipedes (Chilopoda) were also tested.

Fourteen species of Carabidae, three species of Staphylinidae, one species of Silphidae, the cantharid larva, one centipede and unidentified harvestmen had eaten material of slug origin. Within these species the percentage of individuals which had eaten slugs varied from 2% to 100%, and it was found that the larger a species is, the more likely it is to eat slugs. It is possible that the smaller species are scavengers and do not actively predate slugs.

Analysis of results obtained from the most numerous carabid species, <u>Feronia madida</u>, showed that the percentage of its active population eating slugs remained constant, and that the fuller the beetles' crops were the more likely they were to contain slug material.

Theoretical calculations showed that within the family Carabidae only 9% of the adults might be involved in predation. The importance within this percentage of <u>Feronia madida</u> is discussed.

The relative efficiency of the different methods used in this study is discussed and suggestions are made for future studies.

CONTENTS

	Page No.
INTRODUCTION	1
LITERATURE ON PREDATION OF SLUGS	3
INTRODUCTORY STUDIES	5
LITERATURE REVIEW	10
(A) Pitfall trapping	10
(B) The seasonal distribution of coleopterous species	10
Family Carabidae	11
Family Staphylinidae	26
Family Scarabaeidae	28
Family Silphidae	29
(C) Serology	30
METHODS	
(A) Methods used during population survey	31
(B) Preparation of antiserum	41
Preparation of inoculum	41
Immunisation of rabbits	41
(C) Methods used in serological tests	43
Extraction of gut contents	43
Double-diffusion tests	44
Specificity of antisera	45
Sensitivity of tests	47
RESULTS	
(A) Family Carabidae	49
(B) Family Staphylinidae	102
(C) Family Scarabaeidae	103
(D) Family Silphidae	108
(E) Other species	112

Page No.

DISCUSSION AND CONCLUSIONS 115

(A) Feeding trials v. serological tests 115

(B) Beetle size and the percentage of predation 117

(C) Analysis of results of Feronia madida serological tests 119

Seasonal changes 119

Nocturnal/diurnal behaviour 121

Percentage predation and crop distension 123

(D) The significance of predation by adult carabids 125

(E) Possible future studies 132

ACKNOWLEDGMENTS 135

REFERENCES 136

INTRODUCTION

The purpose of this study is to determine the possible effect of invertebrate predators on field populations of slugs, with particular reference to Agriolimax reticulatus.

Slugs are a well known pest which can cause serious damage to plants and crops in gardens and farms. Hunter (1969) estimated that in a normal year in England and Wales slugs were responsible for at least £200,000 of damage to wheat and £650,000 of damage to potatoes. Agriolimax reticulatus is the commonest and most widely distributed British slug, occurring in a wide variety of habitats. When mature it is about 2-3 cm long and is generally cream or buff-coloured. It is active throughout the year, feeding at night above ground on plant material. During the day and when conditions are unsuitable at night it retreats into the soil or under stones and surface debris, where it may feed also.

Because slugs are an important pest there have been many investigations into their control by artificial means, but very little research has been done to discover the significance of natural regulation of their numbers. While it has been assumed that soil invertebrates such as the larger beetles do feed on slugs there has been little experimental work published to confirm this. Because of this lack of knowledge the possible effects of artificial control over a period of time on the natural enemies of the slugs, with the possibility of an upset in the balance existing in the soil between these and other invertebrate populations, has also been largely neglected.

It was obviously impossible to study all possible parasites and predators so emphasis has been placed on the relationships between some of the commoner soil arthropods and slugs after they have developed beyond the egg stage.

The first part of the work consisted of laboratory feeding trials in which arthropods, mostly beetles, were confined with slugs to discover whether or not they would eat them. For various reasons (detailed below) these trials proved unsatisfactory, and the remainder of the work was devoted to sampling in the field to determine the seasonal abundance of invertebrates which might prove to be predators, and to the examination of appropriate gut contents, using serological techniques to determine the presence or absence of slug material in them.

LITERATURE ON PREDATION OF SLUGS

One of the earliest references to invertebrates eating molluscs is found in Taylor (1900). He wrote that the Coleoptera prey freely upon the Mollusca and, without comment, continued with the following quotation: "The Silphidae also destroy the smaller land species, the Rev. A. H. Cooke stating that they fracture the shells by striking them against their own prothorax".

Fowler *et al* (1913) observed *Cychrus rostratus* (= *caraboides*) (Coleoptera Carabidae) feeding on snails, in its larval and adult stages. No details were given of how this was done.

Glendenning (1952) in a pamphlet on slug control in Canada noted that *Carabus nemoralis* had become common in the coastal areas of British Columbia and that it destroyed large numbers of slugs.

Davies (1953) examined the crop contents of British carabids. He noted that molluscs could only be recognised in the contents when fragments of their radulae had been swallowed. He found these in one of eighteen *Feronia madida* examined and in two of twelve *Abax parallelopipedus*.

Linssen (1959) described how two silphid beetles *Phosphuga atrata* and *Ablattaria laevigata* attack and eat snails. He quoted the work of Vogel (1915) who showed how the larva of the glow-worm *Lampyris noctiluca* (Lampyridae) kills slugs and snails by secreting digestive juices into their tissues and sucking up the liquid.

Stephenson (1964) reported that the carabid beetles *Carabus violaceus*, *Feronia madida*, *F. nigra*, *F. vulgaris*, and *Abax parallelopipedus* would eat slugs when artificially confined with them in laboratory tests. *Harpalus rufipes* and *Nebria brevicollis* did not attack slugs. This report will be discussed in more detail later.

Stephenson *et al* (1966) reviewed many of the papers published between 1921 and 1965 on the relationships between slugs and other invertebrates. Most of these refer to parasites or predators from the Protozoa, Platyhelminthes and Nematoda, however twelve insect species are given. These, apart from those mentioned above, are: Diptera. Calliphoridae. *Sarcophaga melanura* larvae. Sciomyzidae. Larvae of *Tetanocera plebeia*, *T. valida*, *T. clara*, and *T. elata*. Phoridae. Unknown species of larvae in *Agriolimax laevis* eggs. Coleoptera. Lampyridae. *Phausis splendidula* larvae. Carabidae. Adult *Scaphinotus interruptus* (in the U.S.A.).

INTRODUCTORY STUDIES

Introductory experiments were made to determine which, if any, of the soil invertebrates occurring locally would eat slugs given the opportunity.

A variety of beetles were caught and confined with slugs in plastic boxes 12 cm square, at room temperature. These were examined regularly to discover if the slugs had been eaten. The duration of these experiments varied greatly depending on whether the beetles died naturally or not, the shortest being for 8 days and the longest for 177 days.

Originally the boxes were half full of soil, with a piece of damp moss to keep the air moist and some lettuce or cabbage as food for the slugs. However, it was found that if the beetles were hungry enough they also would eat the plant material, and that if the soil was too shallow the slugs were able to crawl up on to the sides of the box or on to the lid, where the beetles were unable to attack them. Thus in later experiments the boxes were filled nearly full of soil and were without food for the slugs. Subsequent tests indicated that hungry beetles might chew the soil and live, presumably, by eating bacteria and other microscopic organisms. When sawdust was substituted for the soil the slugs appeared to dislike moving on it, climbing up on to the sides and top of the boxes.

Two types of trials were carried out. In the main trials records were kept of the number of slugs added to the boxes and the approximate length of time they remained alive were recorded. In the second type 'spot' tests were carried out in which slugs were added and left for several days before examination.

Using these methods feeding trials were made using the following invertebrates: Coleoptera. Carabidae. 1 Carabus arvensis, 3 C. catenulatus, 3 Cychrus caraboides, 6 Feronia madida, 19 F. nigra, 23 F. vulgaris, 12 Nebria brevicollis, 2 Nebria sp. larvae, 1 Clivina fossor, and 1 Calathus fuscipes. Staphylinidae. 2 Staphylinus erythropterus. Silphidae. 4 Necrophorus vespilloides and 1 N. investigator. One unidentified centipede was also tested.

In the first type of trial graphs of the length of life of the individual slugs in each box can be made and an estimate of their mean length of life when confined with different species obtained. (Figures 1, 2 and 3). Figure 1 shows the 'pattern' obtained when slugs were confined with two adult Feronia nigra, which ate them regularly, Figure 2 shows that an adult Carabus catenulatus ate no slugs, while Figure 3 shows a graph for one Cychrus caraboides, a beetle which is known to eat slugs.

The mean times thus obtained were : F. nigra 2 days, F. vulgaris 3 days, C. caraboides 3 days, N. brevicollis 5 days, F. madida 8 days, and C. catenulatus 12 days. In controls where slugs were kept alone in boxes the average life was 12 days. These numbers were, of course, influenced by the number and size of slugs present in each box and by the rate at which the beetles could capture and digest them.

From these times a list of species in order of ability to prey on slugs can be made.

1. F. nigra 2. C. caraboides and F. vulgaris 4. N. brevicollis 5. F. madida and only doubtfully C. catenulatus.

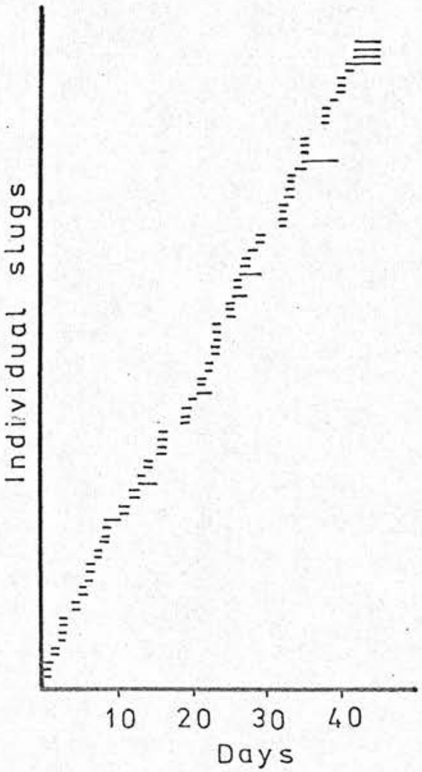

Figure 1

Feronia nigra

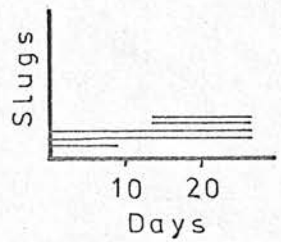

Figure 2

Carabus
catenulatus

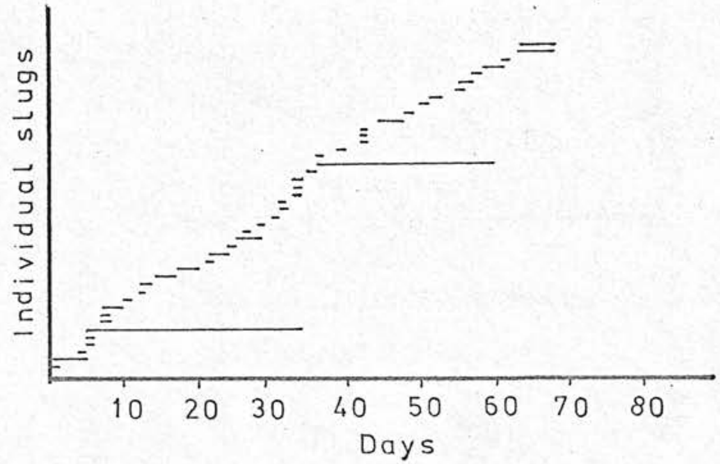

Figure 3

Cychrus caraboides

Figures 1-3: Length of life of individual slugs in feeding trials

In the 'spot' tests Carabus arvensis was observed to eat slugs while Nebria sp. larvae, Clivina fossor, Necrophorus vespilloides, N. investigator, Calathus fuscipes, and the centipede did not.

It was possible that the adult Staphylinus erythropterus fed on dead slugs.

One Necrophorus vespilloides apparently left three bite marks on an Agriolimax reticulatus which was at first affected with abnormal movement, but later, as the cuts healed the slug behaved normally. None of the remaining three N. vespilloides was seen to attack or leave definite evidence that they had attacked slugs. It is possible, however, that one Arion circumscriptus was slightly damaged and perhaps buried in the soil.

Having obtained these tentative results it was realised that the methods used were very rough and ready and that, for the following reasons, any conclusions drawn from the results would be suspect.

Primarily, data obtained by confining hypothetical predators with slugs under laboratory conditions would give no true indication of the situation in the field. A starving beetle might eat a substance it would not normally eat, and the slugs would perhaps be unable to take normal evasive action if confined in a small box. It is extremely unlikely that a predator would not have a choice of food in the field, and it was thought that a study of food preferences, in the laboratory, would lead the general trend of the study away from its main purpose.

Another objection to this simple scheme of feeding the beetles was that even in an experimental box where only soil is used it is often difficult to be certain of finding all the slugs which were still alive. This becomes more difficult when vegetation has been added. The slugs can curl up in the earth with grains of soil adhering to them and thus be well camouflaged. While the use of sawdust helped overcome this difficulty the slugs, as mentioned above, disliked moving on it and crawled out.

The constant examination of the cultures could have disturbed any balance which might have developed between predator and prey, and it did break up tunnel systems and 'cells' made by the beetles.

The beetles used in these tests were collected during the summer and fed on meat in the laboratory until the numbers were sufficient to start the experiments. It was not realised at the time that beetles which were near the end of their natural life were being used, and in several cases they had been kept alive several weeks longer than might have been expected under field conditions. It is possible that their behaviour was abnormal.

Finally, there was no definite proof that when a slug was recorded as being absent from a box it had in fact been eaten by the 'predator'. Slugs which have died naturally decompose or dry up quickly and can be overlooked, and despite precautions some slugs might have escaped. Examination of gut contents was of little use as a slug has very few recognisable features after it has been eaten. (The hard shell and radula may not be ingested). Also, several of the species tested are known to be liquid feeders (i.e. have pre-oral digestion) and so their gut contents are visually unidentifiable.

Thus after these initial tests it was realised that a different approach to the study was necessary: Firstly, it was assumed that most slugs would be attacked by predators on the surface of the soil at night, so a survey would need to be made to discover which invertebrates would be commonly on the surface at different seasons. Pitfall traps were sunk in several different habitats and visited throughout one year to determine this.

Secondly, to discover whether slugs were being eaten in the field it was decided to keep laboratory tests to a minimum, and to trap invertebrates at times and in places indicated as most suitable by the survey, and to examine their gut contents. The only certain way of determining the presence or absence of slug tissues in these gut contents is by serological tests, so a technique was developed for this purpose.

LITERATURE REVIEW

(A) PITFALL TRAPPING

A pitfall trap is a container, such as a jar or tin can, sunk in the soil so that its top is level with the surface. Non-flying invertebrates may fall into it and be unable to escape.

Briggs (1961), Mitchell (1963) and Greenslade (1964) made studies of the efficiency of this method of trapping when used for carabid beetles. They found it of little value for estimating the absolute size of populations or for comparison of communities from different types of habitat. The efficiency of the trap was influenced by the nature of the surrounding vegetation and the ease with which the beetles could move through it, the soil moisture, and the differing behaviour of the different species of beetles.

They all agreed, however, that this type of trapping is useful in the study of distribution, seasonal abundance and behaviour such as the daily rhythm of activity, if the results are used as a guide and too much emphasis is not put upon any differences which may occur.

(B) GENERAL BIONOMICS OF COLEOPTEROUS SPECIES

The following literature review refers to the species which were tested in the laboratory for the presence or absence of slug tissue in their gut contents.

There are two papers of importance in connection with the seasonal occurrence of soil invertebrates, with particular reference to beetles, which come within the scope of the present study. Firstly, Hussey and Lane (1956) used three baited and one unbaited pitfall traps at each of four sites, for one year, in the same area of Midlothian. They listed the species trapped and gave the numbers of each caught at the different sites.

Secondly, Greenslade (1965) studied the ecology of carabid beetles which were trapped at Silwood Park, Berkshire, from 1958 to 1961. He reviewed and summarised earlier papers by himself and by several workers in England and in Europe. Further references will be made to these papers later.

Family Carabidae

Genus Carabus

Carabus arvensis Herbst

Neither Hussey and Lane (1956) nor Greenslade (1965) record having trapped this species.

Carabus catenulatus Fabricius

Hussey and Lane (1956) caught none of this species in mixed hardwood, but twenty-five in a pure spruce wood, one in an open hill field and twenty in hill pasture.

Greenslade (1965) found adults from April to November, with a peak of activity in September and none in July and August. He stated that it was a predominantly larval overwintering species although hibernating adults were found in his area and elsewhere. He found larvae in April. Van der Drift (1951) in Holland found adults emerging in May and June, aestivating during the following two months and reappearing to breed in the autumn. Lindroth (1945-49) in Sweden recorded a single adult peak in July.

Greenslade recorded C. catenulatus as a woodland species, but characteristic of bracken and scrub on the edge of woodland rather than in deep shade. He found it to be nocturnal.

Carabus nemoralis Muller

Kevan (1945) found the species in an Edinburgh suburban garden.

Glendenning (1952) noted that C. nemoralis destroyed large numbers of slugs in British Columbia.

Davies (1953) examining crop contents found that the three adult C. nemoralis he examined contained liquid red or brown food. He classified the genus Carabus as liquid feeders, which were probably carnivorous.

Hussey and Lane (1956) working in the same area as the present study, and using baited traps, caught no C. nemoralis in a mixed hardwood area or in a pure spruce wood, one in an open hill field and six in hill pasture.

Greenslade (1965) trapped only a few adults from February until November, with a peak in May and another in October. He quotes Van der Drift (1951) finding similar maxima in Holland.

Greenslade also quotes Hikimiuk (1948) who when working near Moscow found that only 70% of the spring adults emerged in the autumn, after summer inactivity. He regarded nemoralis as a forest species. Lindroth (1945-49) in Sweden found a main peak of activity in June, with numbers falling in July and increasing slightly in August.

Greenslade himself found C. nemoralis to be a nocturnal grassland species. Kirchner (1960) in Germany and Hikimiuk in the U.S.S.R. found it nocturnal also, while Krumbiegel (1932) described it as nocturnal in North and East Europe, and diurnal in the South.

Carabus violaceus Linnaeus

Davies (1953) examined six crop contents from C. violaceus. He found one crop empty and five containing dark red or brown liquid food. One also contained arthropod fragments. In 1959 he included young harvestspiders, rotting apples and arthropods in this species' food list.

Hussey and Lane (1956) caught one specimen in pure spruce and one in hill pasture.

Williams (1959b) trapping near Reading, makes no mention of catching any Carabus sp. adults.

Stephenson (1964) found that in the laboratory one adult ate five A. reticulatus in four days.

Greenslade (1965) trapped adults from June to September with a maximum in July. Larvae were caught in late September and October. He quoted Tipton (1960) recording a June-July maximum near Reading. Van der Drift (1951) in Holland found that the first few adults which appeared in early summer were females which had survived the winter. Later in the summer came the major emergence of the generation which had hibernated as larvae. Greenslade said that in Denmark the maximum also occurred in June and July, and in Sweden from June to August. At Silwood he found the species to be widely distributed, nocturnally active, and occurring in woodland, arable land and grass heath.

Pollard (1968a) classified C. violaceus as a field species with no apparent association with hedges.

Genus Cychrus

Genus Cychrus

Cychrus caraboides (Linnaeus)

Donisthorpe (1913) observed larvae and adult C. caraboides eating snails but gives no details of how this was done.

Kevan (1945) found the species in an Edinburgh garden.

Davies (1953) examined the crop of one beetle and found it contained liquid food. He assumed the beetle was carnivorous.

Hussey and Lane (1956) caught one adult in hill pasture, but none in mixed hardwood, pure spruce or open field sites.

Greenslade (1963) caught adults in traps set in beech litter and bracken but not in those in grass heath. In 1965 he noted that adults had been found from June to September, and that no larvae were found. Lindroth (1945-49) is quoted in this paper as saying that the species overwinters as the larva with adults emerging and breeding from mid-summer. Greenslade classifies the species as nocturnal and woodland.

Genus Feronia (= Pterostichus)

Feronia adstricta (Eschscholtz) and Feronia anthracina (Illiger)

Neither Hussey and Lane (1956) nor Greenslade (1965) recorded these species.

Feronia diligens Sturm

Hussey and Lane (1956) did not trap this species.

Dawson (1965) found that the adults overwinter, emerge from April onwards and breed in the spring. Larvae occur in the summer and new generation adults may be active in July. She presumed that the species was a scavenger.

Greenslade (1965) found it in damp places, and assumed the species was nocturnal.

Feronia madida (Fabricius)

Kaufmann (1937), in Yorkshire, using only two traps baited with meat caught a total of 1,374 Feronia madida from March to December, with peak numbers in July and August.

Kevan (1945) found F. madida in an Edinburgh garden.

When Davies (1953) examined the gut contents of eighteen he found fragments of molluscan radulae in one only. He concluded that unspecialised feeding habits were partly responsible for the species' abundance around human habitations, particularly in town gardens. In another paper on beetles' food preferences Davies (1959) noted that there were records of the beetle feeding on collembolans, molluscs, earthworms, spores, and other plant material.

Hussey and Lane (1956) caught this species from May to November, with peaks in June and August. One specimen was caught in mixed hardwood, one in pure spruce, forty-five in a hill field and 177 in hill pasture.

Williams (1959b) made a study of the activity of F. madida. He found that the species is nocturnal in woodland and mainly diurnal in open grassland. Experiments showed that it had an intrinsic twenty-four hour rhythm with its active phase at night, but the time of movement could be controlled by manipulating the periodicity of feeding and of light, so if a beetle strayed into another type of habitat it could adapt to the conditions it found there.

In another paper (1959a) Williams had found that there was greater nocturnal activity among fauna living in woods than among fauna in open country, so the timing of the beetles' activity in the different habitats could be related to the abundance or availability of moving prey. He discussed the main objection to this theory which was the assumption that prey was taken while it was moving. Davies (1953) had classified F. madida as a scavenger but Williams thought that his method of examining crop contents gave no indication of the state of the food when eaten. In his opinion the species could be a generalised carnivore and not a scavenger. The fact that it would eat a variety of dead foods in the laboratory did not, in his opinion, give a reliable indication of its food in nature.

Greenslade (1963) found that the beetles from woodland and grassland required a week to achieve the same daily activity pattern.

In 1965 Greenslade noted that adults were caught almost throughout the year with a well-marked peak of activity during July and August. Numbers fell during the winter reaching a minimum in February and March. Larvae were infrequently trapped but their presence was recorded in soil and litter from September until June. New adults appeared in June, July and early August.

The species was widely distributed in woodland and grassland, being most frequent in the latter. Referring again to the different times of activity in different habitats he quoted Kirchner (1960) who found that F. madida was nocturnal in open habitats in Germany. He suggested that the diurnalism and occupation of open habitats, with the advantage of higher temperatures and hence also higher levels of activity were permitted by higher humidities in Atlantic Britain.

Stephenson (1964) found that F. madida (possibly one individual) ate only one Agriolimax reticulatus during fifteen days although it was offered no other food. When six starved F. madida and three F. vulgaris were confined with twenty adult A. reticulatus in a soil-filled arena, 3 feet square, with clumps of grass for cover and sliced carrot as food for the slugs, all the slugs were eaten in twenty-four days. Solitary starved F. madida did not eat A. reticulatus eggs in nine days.

Pollard (1968a) classified the species as a field species with no apparent association with hedges. In another paper (1968b) the peak numbers of his catches in a glade and in a field were in July and August.

Danthanarayana (1969) caught peak numbers in August at Silwood, Berks.

Feronia nigra (Schaller)

Kaufmann (1937), with two traps in Yorkshire, caught one Feronia nigra in July and one other in August.

Hussey and Lane (1956) caught four at their hill field site, but none at the mixed hardwood, pure spruce or hill pasture sites.

Greenslade (1964) quoted Kabacick (1957) in Poland who found that this species is active both on and within leaf litter.

Stephenson (1964) noted that his (possibly one) F. nigra ate only one slug in fifteen days although offered no other food.

Greenslade (1965) trapped adults from April until October with a maximum in August. He found no larvae or callow adults but recorded overwintering adults. He noted that Van der Drift (1951) found callows in July in Holland. Lindroth (1945-49), in Sweden, found a June maximum while Larsson (1939), in Denmark, trapped larvae throughout the year, with most in November, and an

August adult maximum with callows in June and July. Greenslade suggested that the species may be autumn breeding with overwintering larvae; that individuals may breed in two seasons; or that those emerging in one season do not breed until the next season. Finally, he classified F. nigra as a widespread nocturnal species occurring in woodland and grassland, but less frequently on arable land.

Feronia nigrita (Fabricius)

Hussey and Lane (1956) caught three F. nigrita in an open field.

Greenslade (1965) quoted Tipton's report (1960) that the species overwinters as the adult with maxima in March-April and October. He also pointed out that in Denmark there are April-May and August-October maxima, and that in Sweden there is a single activity peak in May-June.

Feronia strenua (Panzer)

Kaufmann (1937) trapped one F. strenua adult in March.

Hussey and Lane (1956) did not catch any of this species.

Boyd (1960) found adults in May and June on Tiree.

Dawson (1965) discovered that the life history of this species is similar to that of F. diligens, except that the new generation adults emerge in August. She thought that it was a scavenger with a very varied diet of animal and plant material.

Greenslade (1965) found F. strenua in damp places and assumed it was nocturnal.

Feronia vulgaris Schaum (= melanaria (Illiger))

Kaufmann (1937) in Yorkshire caught seventy-two Feronia vulgaris from

July to September in two traps.

Hussey and Lane (1956) with twelve traps do not record the species at any of their four sites.

Briggs (1957) found that eggs are laid in August and September. The larvae are present until April and pupate in May. New imagines appear in June and a few adults may overwinter.

Williams (1959a) caught one F. vulgaris in a trap which gave an indication of the time at which any animals trapped in it were caught. This beetle was caught at dusk.

Boyd (1960) working on Tiree caught considerably greater numbers on ungrazed land than on grazed. They were trapped in every month of one year, with a peak in August (581 from ungrazed land and 29 from grazed).

Scherney (1960) found that F. vulgaris formed approximately 20% to 35% of the total carabids he caught over a period of four years in Germany.

Stephenson (1964) found that one F. vulgaris ate five Agriolimax reticulatus in fourteen days. As mentioned above, when three were confined with six F. madida twenty slugs were eaten in twenty-four days.

Greenslade (1965) trapped these beetles from February to October with the maximum numbers between June and August. Larvae were caught in January and October. He found it a nocturnal species of grassland and arable fields. He quotes Larsson (1939) and Lindroth (1945-49) as finding hibernating adults in Denmark and Holland respectively.

Chauvin (1967) mentioned that in France this species begins to predominate among the carabids in June.

Finally, Pollard (1968a) investigating the effects of the removal of bottom flora from hedges caught 25 in a year when the flora was removed and 273 when it was not. However, he classified the species as a field one with no apparent association with hedges. He also found that the number of those beetles in a field fell sharply after harvesting at the beginning of September. (1968b).

Genus Nebria

Nebria brevicollis (Fabricius)

Greenslade (1965) remarked that Nebria brevicollis is the most thoroughly studied British carabid, but as only a small percentage of those caught during the course of the present study were found to have eaten slugs only a few of the relevant papers will be summarised here.

Davies (1953) classified the species as carnivorous, eating a wide variety of food.

Hussey and Lane (1956), using baited traps, caught four N. brevicollis in mixed hardwood, one in pure spruce wood, forty-eight in an open hill field and one in hill pasture. They also caught one Nebria gyllenhali Schonherr in the spruce wood.

Williams (1959a), using a time trap, found that N. brevicollis is strictly nocturnal, having caught eighty-nine at night and only two during the day. He noted that the species would eat a variety of dead food in the laboratory. (1959b).

Greenslade (1965) summarised the life history as follows: it breeds in the autumn and overwinters as the larva; newly emerged adults appear from May to June, show some early summer activity, and then diapause until the main period of reproductive activity which lasts from September until November. Although populations extend into other habitats N. brevicollis is essentially an inhabitant of woodland litter.

Penney (1966) working in south-west Scotland found that the only differences in life history from those reported in England were a later pupation of third instar larvae in spring and consequently a later emergence of the teneral adults. (The difference was about three weeks). There was an activity peak in June with an inactive period until early September. She found that small dipterans formed about 38% of the diet of an adult N. brevicollis, collembolans 32%, mites 23%, spiders 4%, and small earthworms 3%. There was a selection of food up to 4 mm in length.

In 1969 Penney showed that during diapause the population is inactive, aggregated under logs and stones with energy for body maintenance being supplied by the oxidation of their food reserves. Experiments showed that food supply was an important factor in the onset of diapause and she suggested that the ultimate reason for diapause is the avoidance of conditions of low food supply in the sparse woodland litter during the summer.

Genus Calathus

Calathus fuscipes (Goeze)

Davies (1953) classified the genus as liquid feeders presumably carnivorous.

Kevan (1945) found C. fuscipes in an Edinburgh garden.

Hussey and Lane (1956) caught five in an open hill field, five in hill pasture and none in mixed hardwood or spruce.

Boyd (1960), working on Tiree, Argyll, trapped this species from July to December, with a peak of activity in September. He considered that this species, as well as others in the genus, was favoured by grazing of land.

Greenslade (1965) found the species throughout the year, but most commonly from July to September. It was a nocturnal grassland species reaching maturity in August and overwintering as a larva.

Pollard (1968a) caught only two in one year, in an English hedge bottom.

Calathus melanocephalus (Linnaeus)

Kevan (1945) recorded this species in an Edinburgh garden.

Hussey and Lane (1956) caught two in mixed hardwood, one in pure spruce and two in hill pasture. None were caught in an open hill field.

Boyd (1960), on Tiree, found many more on grazed land than on ungrazed, from May to December, with peak numbers in September and October.

Calathus micropterus (Duftschmid)

Hussey and Lane (1956) trapped four adults of this species in mixed hardwood, but none elsewhere.

Calathus piceus (Marsham)

Hussey and Lane (1956) caught six C. piceus at their pure spruce wood site only.

Greenslade (1965) found this nocturnal species in woodland litter. Adults were trapped from April until December, with the greatest numbers from May to August, when there was a peak followed by a sharp decline in numbers in September.

Genus Amara

Kevan (1945) found Amara plebeja, A. bifrons and A. familiaris in an Edinburgh garden.

After examining twenty-four adults Davies (1953) classified the genus as herbivorous.

Hussey and Lane (1956) do not record any species in this genus.

Boyd (1960), in Tiree, trapped three species of Amara from April to October - A. aenea, A. communis and A. bifrons.

Greenslade (1965) discussed A. plebeja, A. communis and A. lunicollis. All occur in grassland or grass heath, overwinter as adults and breed in the spring. Larvae feed throughout the summer and new generations adults appear in the autumn.

Genus Agonum

Agonum mulleri (Herbst)

Davies (1953) classified the genus Agonum as liquid feeding, presumably carnivorous.

Hussey and Lane (1956) trapped one A. mulleri in an open hill field, and none at their other sites.

Scherney (1960), in Germany, found that this species accounted for no more than approximately 5% of the carabids caught.

Greenslade (1965) quoted Tipton (1960) as reporting that this species is a spring breeder with overwintering adults. The numbers caught were greatest in May and again during August-September. Greenslade himself found that it had a wide habitat range, occurring both in damp places and in very dry sandy ones. Overwintering adults were found under bark and similar places in woodland. The species was 'plastic' in its daily activity i.e. it could be nocturnal or diurnal. As no indication was given of the numbers trapped it can be presumed that there were few.

Genus Clivina

Clivina fossor (Linnaeus)

Hussey and Lane (1956) trapped one C. fossor in a spruce wood.

Tipton (1960) found that the adults overwintered and bred in the spring with maximum numbers in April and May. Greenslade (1965) caught adults in pasture and on the edge of woodland. He thought it was a nocturnal species.

Genus Harpalus

Harpalus latus (Linnaeus)

Davies (1953) classified the genus Harpalus as herbivorous.

Hussey and Lane (1956) and Greenslade (1965) did not trap this species.

Genus Leistus

Leistus fulvibarbis Dejean

Davies (1953) classified the genus as carnivorous.

Hussey and Lane (1956) caught one L. fulvibarbis at their mixed hardwood site.

Leistus rufescens (Fabricius) (= ferrugineus (Linnaeus))

Hussey and Lane (1956) did not trap this species.

Greenslade (1965) caught most L. rufescens from late August to December, although callow adults were trapped in May and June. Larvae occurred in January and February. He found that this species is a woodland one, preferring canopied or open areas to leaf litter.

Pollard (1968) classified the species as being confined to the hedge or the region close to it.

Genus Loricera

Loricera pilicornis (Fabricius)

Davies (1953) examined the crops of ten adults and classified the species as carnivorous.

Kevan (1945) found L. pilicornis in an Edinburgh suburban garden.

Hussey and Lane (1956) caught seven in mixed hardwood, one in pure spruce, ten in an open hill field and none in hill pasture.

Boyd (1960) caught nine on ungrazed and none on grazed land on Tiree.

Greenslade (1965) trapped adults from February to August with maximum numbers in April and May. Larvae were recorded from May to July. Tipton (1960) had found most adults in April, a decline in numbers in mid-summer and a slight increase in the autumn. In Sweden Lindroth described the species as overwintering as the adult with only a single peak of activity. Greenslade thought that in Britain overwintering adults bred in the following spring with some surviving through the summer. The next generation of newly emerged adults showed some activity in the autumn before overwintering. L. pilicornis was diurnal at Silwood but had been recorded as nocturnal by Kirchner (1960) in Germany. As the species occurs in a wide range of habitats it is possible that the time of their activity varies with these.

Pollard (1968a) classified L. pilicornis as a field species with no apparent association with hedges, but noted that these could be overwintering sites.

Genus Patrobus

Patrobus excavatus (Paykull)

Neither Hussey and Lane (1956) nor Greenslade (1965) record trapping this species.

Kaufmann (1937) trapped one in August in Yorkshire.

Family Staphylinidae

Genus Philonthus

Philonthus decorus (Gravenhorst)

Hussey and Lane (1956) trapped six P. decorus in mixed hardwood, and one in hill pasture.

Philonthus carbonarius (Gyllenhal)

Kevan (1945) caught this species in an Edinburgh garden.

Hussey and Lane trapped one in hill pasture.

Philonthus intermedius Lacordaire

Hussey and Lane (1956) trapped thirty-three in an open hill field.

Philonthus laminatus (Creutzer)

Hussey and Lane (1956) caught thirty-one in an open hill field and two in hill pasture.

Genus Staphylinus

Staphylinus aenocephalus (De Geer)

Hussey and Lane (1956) trapped two S. aenocephalus at their mixed hardwood site, three in pure spruce, twenty-one in an open hill field and ten in hill pasture.

Boyd (1960), on Tiree, caught this species every month of the year with peak numbers from September to December and again in March. He found that S. aenocephalus occurred in greater numbers on grazed land than on ungrazed.

Genus Quedius

Quedius lateralis (Gravenhorst) and Quedius fuliginosus (Gravenhorst)

Hussey and Lane (1956) did not record these species.

Genus Xantholinus

Xantholinus glabratus (Gravenhorst)

Kevan (1945) found this species in an Edinburgh garden.

Hussey and Lane (1956) caught one X. glabratus in a pure spruce wood.

Boyd (1960) caught *Xantholinus* spp. throughout the year on Tiree. Some of the individuals were doubtfully *X. glabratus*. All the species were favoured by ungrazed conditions.

Genus *Olophrum*

Olophrum piceum (Gyllenhal)

Hussey and Lane trapped six adults in mixed hardwood.

Family Scarabaeidae

Geotrupes stercorarius (Linnaeus)

Aphodius rufipes (Linnaeus)

Hussey and Lane (1956) do not record any scarabaeids.

Ritcher (1958) in a review of the biology of Scarabaeidae noted that the subfamily Geotrupinae feeds on carrion, dung and fungi. The Aphodiinae also feed on these and on decaying vegetable matter.

Family Silphidae

Phosphuga atrata (Linnaeus)

Hussey and Lane (1956) trapped one specimen of this silphid beetle in hill pasture, and none in mixed hardwood, pure spruce or in the open hill field.

Linssen (1959) describes, with illustrations, how P. atrata feeds on snails. The beetle eats its way through the snail's slime apparently with the assistance of a secretion which has a dissolving action that acts not only upon the slime, but also on the snail's tissues. It progresses in this way head first into the shell where it eats the remaining tissues.

R. M. Dobson (personal communication) found that during laboratory feeding trials, using Agriolimax, Milax and Arion species, P. atrata larvae and adults readily ate small slugs.

During this study adult beetles in general were identified with the aid of books by Joy (1932) and Linssen (1959). Fowler (1887) and Fowler (1888) were occasionally used for identifying carabids and staphylinids respectively. The identity of the different species was confirmed by consulting the Waterhouse collection of Coleoptera, which is housed in the Edinburgh School of Agriculture.

The larval carabids were separated, as far as possible, with the aid of van Emden (1942) and Linssen (1959). The Carabus species were identified using Luff (1969).

(C) SEROLOGY

Serological techniques have been used several times in studies of predator/prey relationships, e.g. Brooke and Proske (1946) investigated the predators of mosquito larvae. Fox and McLellan (1956) showed that carabids and staphylinids fed on wireworms, and Dempster et al (1959) proved that carabids preyed on the pupal stage of a chrysomelid beetle. Darthanarayana (1969) similarly found that various carabid and staphylinid species preyed on the larvae of Sitona regensteinensis, the broom beetle.

The techniques used in this study for preparation of antisera were developed from a personal communication by T. W. Tinsley. Crowle (1961) gives details of methods which can be used to test material against such antisera and discusses in detail the interpretation of results so obtained.

One of these methods was used in the present study to test for the presence of slug tissues in invertebrate gut contents. This is the Ouchterlony technique which is based on the principle of double-diffusion through a sheet of agar. In this method a serum containing antibodies against specific antigens is placed in a central well in a dish containing agar and the substances to be tested are placed in wells surrounding it. The serum and the test materials slowly diffuse towards each other. If, when they meet, the antigens to which the serum has been sensitised are present, precipitation occurs along their line of meeting forming an opaque band or bands.

M E T H O D S

(A) METHODS USED DURING THE POPULATION SURVEY

From the first week of March 1968 until the first week of March 1969 regular visits, mostly daily, were made to pitfall traps sunk at five different sites. The traps consisted of white plastic containers $2\frac{1}{2}$ inches across the top, $2\frac{1}{2}$ inches deep and 2 inches across the bottom. In most cases the insides were painted black.

Different numbers of traps were used at the different sites because preliminary sampling had shown that there were fewer beetles at the higher sites. By increasing the number of traps at those sites it was hoped to increase the chances of catching as many different types as possible.

The five sites during this period were in or near the Pentland Hills in Midlothian, and were as follows:

(1) Hillside

Thirty-six traps on an open grassy hillside (Caerketton hill) at approximately 975 feet. (Plates 1 and 2). The traps were sunk in a flat region over an area of about 26 feet by 16 feet. It was heavily grazed by cattle and sheep so the vegetation was short and compact. The main grass was *Agrostis tenuis*, with some *Poa pratensis* plants. Other plants present were *Achillea millefolium*, *Vaccinium* sp. (widespread), *Carex* sp. *Juncus effusus*, *Potentilla verna* and *Trifolium repens*. The soil was sedentary, derived from andesite, diorite and rhyolite. Part of the area became water-logged after prolonged rain or snow.

PLATE 1

Hillside and Lower Hillside sites

PLATE 2

Hillside site

(2) Lower Hillside

Fourteen traps on the same hillside as the above site, at approximately 850 feet, next to a permanent grass field (Leips field, Boghall farm). The traps were sunk in an area about 20 feet square which sloped south. (Plates 1 and 3). The site was mainly well-grazed grass, Agrostis tenuis with Poa pratensis, although in summer and autumn twelve of the traps were shaded by bracken, Pteridium aquilinum. Other plants were Achillea millefolium, Carex sp., Cirsium arvense, Euphrasia sp., Galium saxatile, Trifolium repens, two small clumps of Ulex europaeus, and Viola canina.

(3) Spruce Wood

Ten traps in a wood consisting mainly of Sitka spruce, Picea sitchensis, at approximately 800 feet (Plates 4 and 5). The traps were sunk in a straight line up a 1 in 3 slope, which faced south-east. The first and last were about 36 feet apart. The traps at the lower levels were exposed to the sky and the higher ones were progressively more shaded by the spruce, with an increasing depth of needles covering the soil. There was no vegetation at this site apart from the surrounding trees. Field signs (paw and teeth marks and a large adjacent sett) subsequently indicated that these traps were occasionally robbed and/or removed by badgers which found them a useful source of food, so the numbers of insects recorded was probably artificially low.

(4) Field

Ten traps in a grass pasture field (Hillfield, Boghall Farm) which had barley in the previous year. The site was at about 725 feet, facing

PLATE 3

Lower Hillside site

PLATE 4

Spruce Wood site

PLATE 5

Field site

(Also showing relative positions of
Spruce Wood and Edge of Wood sites)

south-east, with the traps sunk in a straight line up a slope which was approximately 1 in 8. The distance between the first and last trap was 123 feet. The grass was the first year of a long ley and consisted of a rye-grass mixture with white clover (Lolium multiflorum, Lolium perenne, Lolium hybrid and Trifolium repens), with a few plants of Ranunculus repens and Rumex sp. The site was 20 feet from the edge of the field which consisted of a fence and rough ground on the bank of a small burn. This bordered a strip of woodland which joined the Sitka spruce wood farther up the hill. (Plate 5). The flora in the area of the fence was an ash tree (Fraxinus excelsior), a hawthorn tree (Crataegus monogyna), and Cerastium arvense, Chamaenerion angustifolium, Rubus idaeus, Rumex sp., Taraxacum vulgare and Urtica dioica.

(5) Mixed Hardwood

Twelve traps set out in part of a mixed hardwood estate at approximately 600 feet (near Garage Field, Bush Estate). Preliminary trapping in the autumn of 1967 had shown that the numbers of beetles were high here, and at this time the site was a shaded almost vegetation-less leaf-littered clearing between beech trees, with a ditch running across it. In the following winter very high winds blew down all the beech trees surrounding it and the clearing became more exposed to the light, (Plate 6 was photographed in February 1969). During 1968 the ground became progressively colonised by plants and by 1969, when beetles were being trapped for serological testing, it was overrun by long grasses and the number of insects caught fell sharply. (In late '69 and early '70 the fallen tree trunks were finally sawn up and removed, and while

PLATE 6

Mixed Hardwood site

this was happening the site was churned up by haulage vehicles, changing the flora once more). It is probable that the original flora present in early '68 resembled that detailed below for the other mixed hardwood sites. The soil was in part brown earth and in part a thin layer of soil which had developed over what may have originally been a dump for ashes, or clinker, used for making paths.

In 1968/69 the invertebrates which had been trapped were identified in the field, as far as possible, and then released. Only rarely were they removed and killed for identification. It was felt that by replacing them a truer picture of the pattern throughout the year would be obtained than by removing them and perhaps seriously affecting the balance of the population. If it was known that there would be no visits for several days the traps were removed for that time to prevent losses from starvation.

Most attention was paid to carabids. Staphylinids were either recorded by size and general description only or by species if this was readily distinguishable. Other beetles such as cholevids, elaterids or scarabaeids were recorded by family only. Centipedes, millipedes and harvestmen were noted as such only. No count was made of spiders, earthworms or small insects other than beetles which became trapped.

Within the family Carabidae the species smaller than 5 mm were recorded as 'less than 5 mm' and were not usually identified as it was assumed that they would be too small to have any effect on slugs. Where larvae were distinctive in appearance, e.g. Nebria spp., Feronia spp., Cychrus caraboides and Carabus spp. they were named generically. Their lengths were measured to the nearest 5 mm, the only practicable method of measuring living larvae in the field.

Greenslade (1964) found that catches were higher when the vegetation was cleared away for 2 feet from the edge of the traps. However, preliminary trapping in '67 had shown that all the sites, with the exception of the Mixed Hardwood one, were accessible to the public being either near a public right-of-way or near places where 'Sunday-walkers' roamed. Also, farm animals were grazing in most of the areas. Anything unusual such as cleared vegetation, covers to keep rain out of the traps or even vegetation beaten down by one's feet drew attention to the traps and frequently they were disturbed or taken out and broken. Thus every effort was made to keep the sites natural, and except for the Hillside site the traps were painted black inside. This proved quite effective, except of course in snow. By adding the daily numbers of traps from March 6 '68 until February 28 '69 the total possible number was 29,520 and the actual number was 24,836. Therefore 16% of the traps during the year were out of use due to disturbance by people, animals, the effects of the weather (e.g. floating out of waterlogged soil) or were removed during holidays.

Although earlier workers had shown that comparisons between sites could be invalid it was thought that these might be of interest. Two factors influenced the results if the numbers caught were pooled into monthly groups. Firstly, there were the different number of traps at each site in use during each month, and secondly there were the different numbers of days in each month. Conversion factors were calculated in order to standardise the catches as follows:

Table 1 shows the total of traps used each month at the five different sites. It can be seen that there were always many more traps in use at the

TABLE I

(Number of effective traps per site per month with conversion factors)

Month	Hillside	Lower hillside	Spruce wood	Field	Mixed hardwood
1968					
March	935 (0.31)	352 (0.82)	250 (1.15)	257 (1.12)	295 (0.97)
April	1079 (0.27)	405 (0.71)	280 (1.02)	287 (1.00)	325 (0.88)
May	825 (0.35)	359 (0.80)	259 (1.11)	241 (1.19)	269 (1.07)
June	1078 (0.27)	419 (0.68)	297 (0.97)	296 (0.97)	346 (0.83)
July	783 (0.37)	320 (0.90)	209 (1.37)	220 (1.30)	228 (1.26)
August	1111 (0.26)	431 (0.67)	291 (0.99)	310 (0.93)	345 (0.83)
September	815 (0.35)	322 (0.89)	216 (1.33)	230 (1.25)	224 (1.28)
October	1115 (0.26)	433 (0.66)	180 (1.59)	310 (0.93)	289 (0.99)
November	951 (0.30)	378 (0.76)	246 (1.17)	265 (1.08)	256 (1.12)
December	648 (0.44)	252 (1.14)	171 (1.68)	169 (1.70)	167 (1.72)
1969					
January	788 (0.36)	420 (0.68)	258 (1.11)	283 (1.01)	278 (1.03)
February	920 (0.31)	378 (0.76)	260 (1.10)	235 (1.22)	277 (1.04)

Hillside site than at the others, and that any conversion factors derived from a combination of the numbers of traps from all the five sites would be strongly influenced by these larger values. The use of such factors would result in most of the catches from sites which had a smaller number of traps being greatly changed. Thus, in order to change the majority of numbers caught as little as possible, the values from the Hillside site were ignored in the initial calculations, and the mean number of the remaining traps, 287, was taken as an arbitary value. Conversion factors for each month, for all the sites, were calculated by dividing 287 by the number of traps actually used. These factors ranged from 0.27 to 1.72 with a mean of 0.91. (If the Hillside values are excluded the mean is 1.06). Thus the standardised adjusted values shown later in the tables are numbers caught per 287 traps per month.

After March '69 beetles caught at the five main sites were taken into the laboratory for testing. In addition eight other sites were occasionally used in late '68 and '69. There were varying numbers of traps used at each site at different times, often between ten and twenty. The eight sites were:

(6) Upper Hillside

The site was near the Hillside site at approximately 1,025 feet. It consisted of a gently slopingsouth-facing slope which was closely grazed. Agrostis tenuis was the main grass with Poa pratensis and a few more fescue plants than at the other hillside sites. Other plants were Carex sp., Cerastium arvense, Galium saxatile, and Viola sp.

(7) Marsh

A few traps were sunk, in drier weather, in a marshy area near the Hillside site, at about the same altitude, 975 feet. The flora was similar to that site although more rushes (*Juncus effusus*) were present. Also present were *Cardamine pratensis*, *Potentilla verna*, *Taraxacum vulgare*, *Ranunculus repens*, moss, and *Ulex europaeus* bushes round the edge of the site.

(8) Wood area

Collections by hand were made from under stones in the spruce wood at irregular times throughout the year. These stones were at the edge of the wood where it became intergrown with deciduous trees. They were either lying on needle litter, or in grassy clearings, at 800 - 900 feet.

(9) Edge of Spruce Wood

This area was at the edge of the spruce wood, (Plate 5), with lightly grazed grass and some leaf litter from surrounding spruce and deciduous trees. The site was flat and shaded, with sparse vegetation on a brown forest soil derived from hillwash. It was separated from the field with the Field site by a deep ditch. The dominant grass species was *Agrostis tenuis* with *Agrostis stolonifera* and less *Poa pratensis* and *Deschampsia caespitosa*. Also present were moss, seedling *Acer pseudoplanatus*, *Digitalis purpurea*, *Ranunculus repens*, a well-developed but dying *Ulex europaeus* bush, and *Viola canina*.

(10) Field (stones)

Collections by hand were made occasionally from under stones which lay at the edge of the field containing the Field site, and which were over a ditch from the Edge of Spruce Wood site. The flora was mainly rather poorly developed rye-grass mixture, Rumex sp. and Urtica dioica. Parts of the area became waterlogged in wet weather.

(11) Potato Field

This field (Anchordales, Boghall farm) is at 650 feet across a main road from the field with the Field site. The traps were mainly in use after the field was first ploughed and when the potato plants were flowering. Mechanical cultivation of the crop and very dry soil made it impracticable to trap at this site regularly.

(12) Clearing with leaf litter

This site was within 50 yards of the Mixed Hardwood site. It consisted of a clearing with leaf litter and mould from beech trees, tree roots, a few Equisetum sp., one clump of Holcus linatus, a small clump of Pteridium aquilinum, and a little moss. In autumn and winter the site became well-covered with fallen beech leaves.

(13) Clearing with leaf litter and grass

This site was also near the Mixed Hardwood site but consisted of a much deeper leaf litter and mould, with a turf, mainly Holcus linatus, on top. The texture of the site was 'springy' compared with the hard soil in the previous area. Other plants were Oxalis acetosella, moss, and some beech and sycamore seedlings. The site was surrounded by well-developed Pteridium aquilinum, Rubus idaeus and naturalised Rhododendron ponticum.

Occasional collections by hand were made near the hill sites but, in general, these were unsuccessful (i.e. few, if any, beetles were caught).

Hussey and Lane (1956) trapped in the same area in which the present study was made. Their open field site was probably in the field next to the present Lower Hillside site, their hill pasture might be comparable to the present Hillside site, their spruce wood site was in the same wood, and their mixed hardwood site was somewhere in the same estate as the present one. Subsequent results suggested that the two sites were not in exactly similar habitats.

Records were also kept of maximum and minimum temperatures at each site, and a visual measurement of rainfall (the depth of rain in the traps) was made.

(B) PREPARATION OF ANTISERUM

Preparation of inoculum

Approximately 10 g of macerated *Agriolimax reticulatus* tissues were suspended in 50 ml of physiological saline. Aliquots of the suspension were homogenised in an M.S.E. high speed homogeniser for 5 minutes. After this treatment the samples were centrifuged at 3000 revolutions for 20 minutes in an M.S.E. Super Medium Centrifuge to sediment the particulate matter.

The supernatant fluid was clarified through a K3 Seitz filter and then sterilised by EK Seitz filtration. The sterile filtrate was distributed into small volumes for storage at -25'C.

Immunisation of rabbits

A sample of the antigen was dialysed against changes of distilled water at 4'C for 12 hours and then homogenised with an equal volume of Freund's complete adjuvant (DIFCO) by shaking. Two rabbits were inoculated with 1.0 ml of this suspension by intramuscular injection.

After four weeks the sensitised rabbits were reinoculated with 0.5 ml of sterile dialysed antigen, without adjuvant, by the intravenous route. This procedure was repeated on the following day.

Blood samples were taken from the ear veins oneweek later and tested for precipitins against the slug extract, in agar double-diffusion plates (described below). The sera were found to contain precipitins although that from one of the rabbits always produced a stronger reaction.

The animals were resampled in two months and only a slight loss of precipitin content was found.

Further supplies of antiserum were required five months later and a blood sample taken then revealed that precipitin reactions were barely detectable in agar double-diffusion tests.

In view of this the rabbits were restimulated by intravenous injection of 0.5 ml of sterile dialysed filtrate. Both rabbits were reimmunised and one died with symptoms of anaphylactic shock a few hours later. The surviving rabbit was resampled after a week and found to have produced anti-slug precipitins which were qualitively indistinguishable from the original antibodies in agar plate diffusion systems.

(C) METHODS USED IN SEROLOGICAL TESTS

Extraction of gut contents

In the laboratory invertebrates, whose gut contents were to be examined for the presence of slug tissue, were killed by immersion in hot water which was not quite boiling. They were removed immediately so that as little change as possible would occur in the structure of their tissues.

The crop contents of carabids were the simplest to extract from freshly killed adults because when the hind margin of the thorax and the anterior margin of the abdomen are forced apart, the crop is pulled out of the abdomen and can be cut out of the gut. The sphincters at either end tend to stop the contents flowing out.

At first each content was put into 0.2 ml of distilled water, so that if three contents were pooled into one sample 0.6 ml water was used. As contents were only pooled when it was thought that they might be of too small a volume to react in the test this was a self-defeating method and after the first 150 tests the volume of water per sample was kept at a constant 0.2 ml.

The volume of the crop contents was estimated visually and recorded as 'empty', 'half full', 'distended' etc.

Extraction of food from staphylinids proved more difficult. During preparation for the earlier serological tests it was found that the crop was more difficult to extract and unlike that of the carabid did not become distended with food to any great extent, so that only a small volume could be extracted to test. To overcome this the contents from several beetles were pooled. Later it was found that a larger quantity could be extracted from further 'down' the gut and this was done with a pipette. In the earlier tests the results from the staphylinids may therefore be biased towards a negative result.

It was found impossible to extract the gut successfully from silphids or scarabaeids and so in these cases the thorax was cut from the abdomen and gut contents were sucked up by a pipette from inside the thorax and abdomen.

Once the gut contents were in distilled water they were either tested immediately or stored in a deep freeze, where they could be kept successfully for several months at least.

Double-diffusion tests

The tests were made in Petri dishes, 9 cm in diameter, each containing gel-diffusion agar. The ingredients of this agar were as follows: 15 g Davis Standard Agar, 16 g sodium chloride, 50 ml 10% aqueous solution of phenol, 1000 ml distilled water. The phenol prevents the growth of micro-organisms and allows the plates to be kept for a long period of time.

Each plate contained approximately 20 ml of the agar with five holes punched in it. Four of the holes, 7 mm in diameter, were arranged in a square around a central hole 9 mm in diameter. The distance between the centres of the central and outer wells was 10 mm.

Serum was placed in the central hole and the contents which were to be tested were placed in the surrounding ones. If the contents were bulky they were shaken up in the distilled water and the liquid so formed tested.

At least one of the four outside wells in each plate contained a control of known slug antigen. This acted both as a check that the antiserum was still sensitised, and also produced bands which could be compared with any which developed at the other wells. This antigen was made by macerating different sizes of *Agriolimax reticulatus* in phenol saline, centrifuging and using the supernatant. It could be kept successfully for several weeks in a cooled incubator (10'C). In one experiment the slug tissue was sterilised first, but this process must have had a deleterious effect as the resulting precipitin bands were very poorly developed.

In the first tests plates were kept at room temperature, but later it was found that although the precipitin bands took longer to develop it was preferable to keep the plates in an incubator at 10'C. These bands were usually more sharply developed and easier to see. The higher temperature had no deleterious effect on the result of the test, but the agar dried out more easily and the plates could not be kept so long. The plates in the incubator were kept for one month and examined regularly by holding them over a bright light.

Specificity of antisera

Various tests were made to discover how specific the antisera, which had been produced by the injection of Agriolimax reticulatus, were.

Serum from a normal unsensitised rabbit was tested against slug antigen and no precipitin bands developed.

Plates 7 and 8 show the results when Agriolimax reticulatus, A. laevis, Arion hortensis, A. ater, and Limax maximus were tested. All showed a positive reaction although one can see that more lines developed with A. laevis, a species in the same genus. Thus the test could not distinguish between species of slugs.

Gut contents from beetles which were observed to eat slugs in the laboratory were tested and proved positive, (Plate 9), while contents of beetles which were known not to have eaten slugs (but had eaten dog food) proved

PLATE 7

1. A. hortensis   2. A. reticulatus

4. A. ater   3. A. laevis

PLATE 8

1. A. hortensis   2. A. reticulatus

4. L. maximus   3. A. laevis

PLATE 9

1. expt. F. madida   2. expt. F. madida

4. control antigen   3. expt. F. madida

negative. Thus the digestive processes had not changed the slug very much while it was in the crop, and the serum was not reacting to some substance present in the beetle gut itself.

Two further experiments were made to discover whether the test could distinguish between 'fresh' and 'dead' slug tissue, and also whether the use of phenol saline or distilled water as a dispersal medium influenced the development of precipitin bands. The slug used was a small dead A. reticulatus which, although it still had its basic shape, was 'melting', or decomposing, round the edges and broke up when shaken in the different media. Plate 10 shows the results when it was mixed with phenol saline, and Plate 11 when it was in distilled water. Bands developed with both but were stronger with the water. Thus the test would not distinguish between slugs eaten alive and slugs which had been scavenged. The stronger development of bands with the water was satisfactory as this was the medium used for testing the gut contents.

To discover whether precipitin bands developed in the presence of snail tissue, snails were collected from limestone strata seven and nine miles from the sites where the present studies were being made. The snails were divided into four samples as follows: (a) Cepea nemoralis, (b) Hygromia striolata and H. hispida, (c) Oxychilus sp. and other small species, and (d) Discus rotundatus. The samples were prepared in phenol saline in the same way as for slugs, and in the subsequent tests the sera reacted positively.

Extensive field observations, including searching under stones and under boards used for trapping slugs, showed that there were very few snails present at the sites used, and that even if beetles did eat snails they would only form a very small part of their diet. If a similar study were made in an area where snails were more numerous, such as in the limestone area where the snails were collected for the tests, one could only state with certainty that the beetles had been eating molluscs. This distinction between slugs and molluscs in general would be important where Phosphuga atrata and Cychrus caraboides occurred as they are known to be adapted for feeding on snails; but the significance of the distinction for other species of beetles is not known.

The sera were tested against small earthworms and enchytraeids, which are known to figure in the diet of many of the larger soil invertebrates, but they did not react against these. One batch of serum was found to react in an unusual manner to enchytraeids when in the presence of slug materials. This was not duplicated with other batches of the same serum and it was decided that this was a spurious reaction due to the fact that that particular bottle of serum had been frozen and unfrozen many times, and was several months old. Crowle (1961) notes that individual serum can react in an abnormal way.

PLATE 10

Dead A. reticulatus in phenol saline

PLATE 11

Dead A. reticulatus in distilled water

Sensitivity of the tests

Tests were carried out to find the sensitivity of the sera, i.e. to find the point at which there would be too little slug material present to be detected. Two A. reticulatus were chosen which were 6-7 mm at rest and weighed 0.04 mg. 0.2 ml phenol saline was added to a series of bottles in order to make a serial dilution. One slug was chopped up in 0.2 ml phenol saline to be used as the 1:1 dilution. The other was similarly treated and added to one of the bottles, which already contained 0.2 ml, so making the 1:2 dilution. This then was serially diluted, and all the dilutions to 1:1004 were tested.

The characteristic brown colour of the slug extract was lost between 1:8 and 1:16. The dilutions reacted positively until 1:256 which was negative. Thus the sensitivity stopped between 1:128 and 1:256 of the 0.04 mg slug. (An earlier experiment testing the strength of some control antigen faded between 1:64 and 1:128).

Finally, tests were carried out to determine the sensitivity of the sera in relation to the visual classification of the crops mentioned above. Beetles were fed experimentally on slugs and then killed. Their crops were extracted, the extent of their distension classified and their contents tested. With fourteen Feronia madida results were positive from 'distended' down to 'less than half full'. Three samples were tested at the 'almost empty state': one showed negative, one positive, and one negative the first time tested and positive when re-tested. Thus at this volume the limits of sensitivity of the serum, for this species, was reached. The contents of one 'half full' Nebria brevicollis reacted positively and one 'very nearly empty' negatively. The crop contents from one 'distended' Carabus violaceus and from one 'distended' Feronia nigra reacted positively.

INTRODUCTION TO RESULTS

Although in many ways pitfall trapping is an unsatisfactory method for field studies (see Literature Review Page 10) it is the only method available by which regular observations can be made concerning the activity of beetles on the soil surface throughout the year.

The following results show the numbers of beetles trapped per month at each site throughout the year March 1968 to the end of February 1969. They are not meant to be an estimate of the total population of each species at different times of the year nor a definite measure of total activity, but they do indicate the months in which the different species are most active on the soil surface, and therefore could theoretically be preying on slugs.

Explanation of Tables

In the tables showing the results of the 1968/69 trapping survey the first number for each month is the actual number of beetles caught, and the second bracketed value is this number multiplied by the appropriate conversion factor, given in Table 1. (For explanation see Page 37).

In the tables showing the results of the serological tests the following symbols are used:

+ = test positive (slug tissue present)

- = test negative (no slug tissue detected)

? = result of test doubtful

e = crop empty

* = pooled sample (more than one crop content in sample)

In general the tables refer to adult beetles. The results concerning larvae are either given in separate tables or marked "L" when shown in tables with adults of the same species.

RESULTS

The results obtained will be given separately for the different species. The tables referred to in the text will be found at the end of each section concerning one particular genus.

(A) Family Carabidae

Genus Carabus

Carabus arvensis

One female Carabus arvensis was found in May 1967 moving during the day on the open hillside, about half a mile from the Hillside site. In the laboratory it fed on small Arion hortensis, Agriolimax laevis and small A. reticulatus. It laid eggs in May and June, and after feeding exclusively on slugs for fourteen days died in the third week of July. Whether death was due to old age or its diet is uncertain.

No more beetles of this species were caught in '68 or '69. If the diurnal behaviour of the beetle was typical this lack of success could be due either to the species not being present near the hillside sites or to the beetles seeing the traps and deliberately avoiding them.

Carabus catenulatus

In 1968 Carabus catenulatus was caught from July to October. Table 2 shows the numbers trapped at the different sites. The converted values show that the species was commonest in the spruce wood. This agrees with the findings of Hussey and Lane (1956) and Greenslade (1965) who also found it a woodland species. The latter however caught none in July and August. Callow adults were found in late July and early August (1969) which differs from the observations of Van der Drift (1951) in Holland who found adults emerging in May and June before a two month aestivation.

During serological tests in '68 and '69 nine adults were tested individually. (Table 3). Six of these were positive (67%). In 1968 seven other adults were tested in pooled samples of 2, 2 and 3 and these all proved positive.

Carabus nemoralis

In 1968 Carabus nemoralis was trapped from March until July and in October. (Table 4). The species was commonest at the grassy hillside sites, which agrees with Hussey and Lane (1956) and Greenslade (1965).

In 1969 seven adults were tested individually from April to June and in October. (Table 5). Five (71%) were positive. The crops all contained liquid food, similar to that found by Davies (1953). (The two beetles which proved negative had almost empty crops).

Carabus violaceus

During the trapping survey Carabus violaceus was trapped from April to August, with the greatest numbers from June to August. (Table 6). They were trapped on the hillside and in the spruce wood, but not in the field or mixed hardwood. These findings agree with Hussey and Lane (1956) but not with Greenslade (1965). He found the species to be widely distributed in woodland, arable and grass heath, and he also caught considerably more.

The crop contents from two adults caught in 1968 reacted positively to the serological test as did seven in the following year. (Table 7). Thus all nine had eaten slugs.

In the laboratory one C. violaceus ate two small A. reticulatus quickly and efficiently, with little hesitation catching them half way along their body. (After this the beetle was killed and it was confirmed that its crop contents were of slug origin).

Carabus larvae

In 1968 no attempt was made to differentiate the species of Carabus larvae which were trapped from April to October. The greatest number of larvae were caught at the Hillside site. (Table 8).

Nineteen larvae were tested serologically. (Tables 3, 7, 9). The first two caught in August '68 and May '69 were of unknown species and proved negative. This may or may not be a true result due to faulty technique.

Six of the remaining seventeen were Carabus catenulatus and only one had eaten slugs. The species of two other larvae was unidentified, but because they were trapped in June and July they were probably also C. catenulatus. One of these was unfed and the other proved negative. Thus only one out of eight (12%) had eaten slugs.

The nine other larvae were Carabus violaceus and eight (89%) were positive.

While these results may reflect a greater preference for feeding on slugs in C. violaceus they may also be influenced by the size of the larvae, as the following table shows:

C. catenulatus	length(mm)	11	11	12	12	19	22	?	?	
	+/-	-	-	-	-	+	-	-	unfed	
C. violaceus	length(mm)	15	23	23	23	23	24	24	25	26
	+/-	+	+	+	+	+	+	+/-	+	-/+

Carabus sp. larvae are black, well chitinised, aggressive, and are quite commonly caught in pitfall traps. Although it has not been definitely proven, it seems likely that they will hunt nocturnally on the surface of the soil, actively killing slugs and not merely scavenging dead ones.

Carabus spp.

From the preceding discussion of individual species it can be seen that adult Carabus beetles are active from March to October, inclusive, and are all capable of eating slugs. Their numbers are augmented at the appropriate times of the year by the larvae which also may eat slugs. In the laboratory adults were seen to attack small slugs on sight ignoring their slime and almost cutting them in half with their mandibles. This behaviour was very definite as if it were at least a fairly common mode of feeding. It differed from the rather tentative exploratory behaviour found in other species such as Feronia madida or Nebria brevicollis.

TABLE 2

Carabus catenulatus

(1968 trapping: actual & adjusted numbers)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
July	1 (0.4)	0	0	0	0
Aug.	4 (1.0)	0	4 (4.0)	0	2 (1.7)
Sept.	1 (0.4)	0	3 (4.0)	0	0
Oct.	0	1 (0.7)	0	0	0

TABLE 3

Carabus catenulatus

(Serological tests)

	Upper Hillside		Hillside		Lower Hillside		Spruce Wood		Spruce Wood area		Edge of Spruce Wood	
	+	-	+	-	+	-	+	-	+	-	+	-
1968												
Aug.	1	-	-	-	-	1	-	-	-	-	*7	-
1969												
June	-	-	-	-	-	-	-	-	-	-	-	-
July	-	-	-	-	-	-	1	-	1	-	-	-
Aug.	-	-	-	-	-	-	-	-	2	-	-	-
Sept.	-	-	-	-	-	-	-	-	-	-	-	-
Oct.	-	3L	-	1L	-	-	-	-	-	-	-	-

* = pooled samples, L = larva

TABLE 3 contd.

	Mixed Hardwood leaf litter		Mixed Hardwood litter & grass		Mixed Hardwood area	
	+	-	+	-	+	-
1968						
Aug.	-	-	-	-	1	1
1969						
June	1L	-	-	1L	-	-
July	-	-	-	-	-	1
Aug.	-	-	-	-	-	-
Sept.	-	-	-	-	-	-
Oct.	-	-	-	-	-	-

L = larva

TABLE 4

Carabus nemoralis

(1968 trapping: actual & adjusted values)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
March	2 (0.6)	0	0	0	0
April	4 (1.1)	1 (0.7)	0	1 (1.0)	0
May	0	3 (2.4)	0	0	0
June	1 (0.3)	2 (1.4)	0	0	3 (2.5)
July	1 (0.4)	0	0	0	1 (1.3)
Aug.	0	0	0	0	0
Sept.	0	0	0	0	0
Oct.	3 (0.8)	1 (0.7)	0	0	0

TABLE 5

Carabus nemoralis

(Serological tests)

	Lower Hillside		Edge of Spruce Wood		Mixed Hardwood 1968 site		Mixed Hardwood leaf litter & grass	
	+	–	+	–	+	–	+	–
April	1	1	–	–	–	–	–	–
May	–	–	1	–	–	–	1	–
June	–	–	–	1	1	–	–	–
July	–	–	–	–	–	–	–	–
Aug.	–	–	–	–	–	–	–	–
Sept.	–	–	–	–	–	–	–	–
Oct.	–	–	–	–	–	–	1	–

TABLE 6

Carabus violaceus

(1968 trapping: actual & adjusted numbers)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
April	1 (0.3)	0	0	0	0
May	0	1 (0.8)	0	0	0
June	4 (1.1)	0	0	0	0
July	5 (1.8)	0	0	0	0
Aug.	3 (0.8)	1 (0.7)	1 (1.0)	0	0

TABLE 7

Carabus violaceus

(Serological tests)

	Upper Hillside		Hillside		Hillside marsh		Hillside area		Lower Hill-side area		Spruce Wood area	
	+	-	+	-	+	-	+	-	+	-	+	-
1968												
Aug.	-	-	-	-	-	-	1	-	1	-	-	-
1969												
June	1	-	-	-	-	-	-	-	-	-	-	-
July	1	-	3	-	1	-	-	-	-	-	1	-
Aug.	-	-	-	-	-	-	-	-	-	-	-	-
Sept.	-	-	-	-	-	-	-	-	-	-	-	-
Oct.	-	-	6L	1L	1L	-	-	-	1L	-	-	-

L = larva

TABLE 8

Carabus spp. larvae
(1968 trapping: actual & adjusted numbers)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
April	0	1 (0.7)	0	0	0
May	0	1 (0.8)	0	0	0
June	1 (0.3)	4 (2.7)	0	0	0
July	0	0	0	0	2 (2.5)
Aug.	1 (0.3)	0	0	0	0
Sept.	11 (3.8)	0	0	0	0
Oct.	29 (7.5)	2 (1.3)	0	0	0
Nov.	10 (3.00)	0	0	0	0

TABLE 9

Carabus spp. larvae (unidentified)
(Serological tests)

	Lower Hillside		Edge of Spruce Wood		Mixed Hardwood litter & grass			area	
	+	-	+	-	+	-	e	+	-
1968									
Aug.	-	-	-	-	-	-	-	-	1
1969									
May	-	-	-	1	-	-	-	-	-
June	-	-	-	-	-	-	1	-	-
July	-	1	-	-	-	-	-	-	-

Genus Cychrus

Cychrus caraboides

In 1968 seven adult Cychrus caraboides were caught in the pitfall traps from June to September, and eight larvae from October to December. They occurred at all the sites except the Spruce Wood. (Table 10). The small numbers trapped are comparable to those of Hussey and Lane (1956) who caught one adult and of Greenslade (1965) who caught five from June to August.

Four other adults were caught, in 1968, three in the Hillside area and one at the edge of the spruce wood. When their crop contents were tested serologically it was found that three had been eating slugs, and the remaining one had an almost empty crop.

In 1969 nineteen adults and five larvae were tested serologically and the results of these tests give some indication of the timing of the species' life-history in the area under study. (Table 11). Greenslade found no larvae but quoted Lindroth (1945-49) as saying that Cychrus overwinters as a larva emerging in mid-summer, as an adult, to breed. While the present work confirms the fact that the larvae overwinter it was also found that adults can hibernate.

One such adult was found in March in a 'cell' hollowed out in a block of peat in a garden about two miles from the trapping sites. It was scratched and dull and obviously an old adult. It was immobile when caught but became active at room temperature. Its crop was quite full of a white material totally unlike the reddish brown liquid which is liquefied slug. This reacted negatively when tested serologically.

Another beetle was also caught in March in the spruce wood area in a cell formed in the soil under a stone. The contents of its half-full crop also proved negative.

No Cychrus were trapped or caught by hand in April.

In May two adults were caught by hand. One from the mixed hardwood area had a crop full of slug material, while the other, from the sprucewood area, was negative when tested. (The volume of the contents from this individual was not recorded but the crop may have been almost empty).

During July, August and September five adults were tested and proved positive.

In October ten Cychrus were caught at the same time under stones in the spruce wood area. Eight of these were in cells under one large stone, with empty or nearly empty crops. The two others, also with almost empty crops, were caught under other stones. One of the ten crops held slightly more fluid than the others, but not enough to react in the test. The other nine crops were washed out in water and tested. A very faint line developed, showing that traces of slug material had been present.

From these findings it would seem that adult beetles can hibernate until some time in May when they become active and start feeding on slugs. Presumably these beetles will die during the following summer after breeding. In the preliminary feeding trials two adults laid eggs in mid and late August and died shortly afterwards. The new generation adults, which have developed from larvae which also have overwintered, will prepare for hibernation by making cells in the soil during October.

Five Cychrus larvae were caught in pitfall traps in late October, three at the Hillside site and two at the edge of the spruce wood. All five had eaten slugs.

To summarise, of the eleven adults which were neither hibernating nor preparing for hibernation eight, or 73%, had been eating slugs before being caught, as had all of the five larvae.

These findings confirmed the observations by previous workers that C. caraboides fed on molluscs, or slugs at least. During the first ten days of a feeding trial two beetles were offered chopped-up earthworm and liver (a favourite food of Feronia and Carabus) and showed no interest in them. They were offered four small snails and the contents of one of these shells were extracted. (It is possible that the shells were too small for the beetles to feed successfully from them). After these ten days, in which only the small snail was eaten, slugs were added regularly to the culture and the beetles survived for about fourteen weeks, only dying after one had laid eggs and they presumably had reached the end of their natural life-span. Another adult stayed alive about eleven weeks on an exclusively slug diet and also died after laying eggs.

This species would appear to be a very specialised feeder which will not adapt to other foods. As it is nocturnal it was never observed feeding but circumstantial evidence suggests that the beetles subdue the slugs with an anal discharge, from pygidial glands (Imms 1964), which in some way partially liquefies the tissues. This treatment also preserves them to some extent as they can remain in a culture for several days without fungi growing on them. The beetles presumably can then feed on the slugs at their leisure.

The experimental beetles ate small Agriolimax reticulatus, A. laevis, Arion fasciatus and A. hortensis, although the Arion species remained longer in the culture before being killed. This could in some way be connected with their tougher, more 'leathery' skin.

Although it is not known definitely how long food remains in the crop after ingestion certain tentative conclusions may be made by examining the state of distension of the crops of the beetles caught in the field. As discussed above, the percentage which had eaten slugs during the time of adult activity was 73%, or eight out of eleven. Two of the three remaining adults were found under stones and had almost empty crops, so probably they had not been active and feeding the night before. (The third was trapped in a pit-fall trap but no record was made of the state of its crop). It would seem therefore that seven of the eight adults which had been active before being caught had eaten slugs, another strong indication that this species feeds exclusively on these.

TABLE 10

Cychrus caraboides
(1968 trapping)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
June	0	0	0	1	1
July	0	2	0	0	0
Aug.	1	0	0	1	0
Sept.	1	0	0	0	0
Oct.	1L	0	0	0	1L
Nov.	2L	1L	0	0	1L
Dec.	0	0	0	0	2L

L = larva

TABLE 11

Cychrus caraboides
(Serological tests)

	Hillside		Lower Hill-side area		Spruce Wood area		Edge of Spruce Wood	
	+	−	+	−	+	−	+	−
1968								
Aug.	−	−	2	0	−	−	0	1
1969								
March	−	−	−	−	0	1	−	−
April	−	−	−	−	−	−	−	−
May	−	−	−	−	0	1	−	−
June	−	−	−	−	−	−	−	−
July	*2	0	−	−	1	0	−	−
Aug.	−	−	−	−	−	−	−	−
Sept.	−	−	−	−	1	0	−	−
Oct.	3L	0	−	−	(9)	1	2L	0

	Mixed Hardwood 1968 site		area		Garden	
	+	−	+	−	+	−
1968						
Aug.	−	−	−	−	−	−
1969						
March	−	−	−	−	0	1
April	−	−	−	−	−	−
May	−	−	1	0	−	−
June	−	−	−	−	−	−
July	−	−	−	−	−	−
Aug.	1	0	−	−	−	−
Sept.	−	−	−	−	−	−
Oct.	−	−	−	−	−	−

( ) * = pooled sample   L = larva

Genus Feronia

Feronia madida

Pitfall trapping

In 1968 735 Feronia madida adults were trapped from March to November with the greatest numbers in July and August. (Table 12). This activity peak agrees with the findings of previous workers. In 1969 one callow adult was caught in the middle of August, slightly later than Greenslade (1965) recorded in the South of England.

The species occurred in a wide variety of habitats being caught at all the sites, but was commonest at the Mixed Hardwood site, with the Lower Hillside second. The low catch in the Spruce Wood, five as against 467 at the Mixed Hardwood, may be partly attributable to the robbing of the traps by badgers, which was mentioned above.

Serological tests

During 1968 the crop contents of 121 F. madida were tested serologically. Most of these were pooled into samples of varying volumes, and so, apart from showing that the species did eat slugs, detailed analysis of the results was impossible.

In 1969 388 crop contents were tested. (Table 13). Until the beginning of June these were also sometimes pooled, but the difficulties in interpreting results presented by this method were by then realised and attempts were made to test each content separately. An exception was made when the volume of food in different crops was so small that it was thought there was not enough material present to react successfully in the tests alone and several contents were then pooled.

Even in these cases the pooling of contents caused difficulties in the interpretation of results: If three contents were pooled together and the test proved negative one knew that all three were negative. But if the test was positive any or all three could be positive. The method of tabulation finally used was as follows: As with other species the results of the serological tests could be 'positive', 'negative' or 'doubtful'. In samples from more than one individual when the result was negative the number of individuals in the sample was recorded as negative, e.g. if there was a pooled sample of three crop contents which proved negative three negative results were recorded. If, however, a sample of three proved positive one could only be certain that a single crop was positive, so one positive and two doubtfuls were recorded. This method results in an underestimation of the percentage positive, but it was felt that this would be preferable to classifying all the contents as positive, or even omitting the results of such tests, which would result in an even stronger bias towards negative results.

Table 13 shows the results obtained from the beetles caught at all the sites used. 76 out of 388 (20%) were definitely positive.

As will be discussed later, a slug is a comparatively large source of food for a F. madida and once a beetle starts to eat one it tends to fill its crop with tissue, and having done so it would not be likely to eat a large amount of other food such as insects. (Conversely, if it had eaten a large amount of other food it would be unlikely to eat much slug material). Because of this the occurrence of a large amount of chitin in a full crop which is found to contain slug tissue can suggest that the beetle has eaten another invertebrate which had fed on slugs. This happened with at least eleven of the positive samples. Two beetles in June and one in October had probably eaten Carabus larvae (while being taken to the laboratory). Four of the others had large amounts of chitin and the remaining samples consisted of material which did not look like slug tissue. Of these two were green, one purple-red and one was a milky fluid with compact material in it.

Feeding trials

In July and August three small feeding trials were made in the laboratory using F. madida and Agriolimax reticulatus. As there are no records of how this species eats slugs under field conditions the following observations may give some indication of this.

In the first trial ten beetles were placed individually in 9 cm Petri dishes with damp sawdust and two small slugs and watched for one hour. (The slugs were approximately 5.0 to 7.5 mm when stretched out). Eight out of the ten immediately attacked the slugs, one attacked within the hour, and the remaining one did not attack at all during this time. The beetles seemed to be attracted to the slugs by their movement.

Four of the adults were killed when the hour had passed and their crop contents were examined and tested. Two had crops full of slug tissue, which differed slightly in colour and texture, the one being slimier than the other. The remaining two beetles had half-full crops, although by examining their dishes it had been assumed that they had eaten one and one and a half slugs respectively. It would seem that they had only eaten parts of the slugs, and the remaining parts had become covered with sawdust. This shows how a false estimate of how much beetles are eating can be drawn by only counting the slugs left in the dishes.

In the second trial ten beetles were placed in separate dishes, nine with one small slug, and one with two very small ones. They were observed for $\frac{3}{4}$ hour and then left for about eighteen hours.

In the first minutes many of the beetles attacked the slugs and became smeared with slime on their mandibles, antennae and, occasionally, their legs. The slugs stuck to the mandibles of two of the beetles which became very distressed, running around trying to dislodge them by movement, or levering them off against the sawdust. Often when a beetle managed to dislodge one it picked it up again. After beetles first encountered and bit at a slug they tended to change their behaviour and go into a 'searching' pattern of behaviour, running round the dish waving their antennae.

One beetle was more successful than the others and bit the slug almost in two about half way along its body. It then removed and ate parts of it. This beetle was very active compared with the others, and tried to lever off the lid of its dish.

Another beetle definitely avoided its slug, cleaning itself immediately it touched it, which happened several times, apparently be accident.

One beetle showed no interest in its slug at all.

In one dish a very small slug was added in addition to the larger one already present. The beetle stood on it, presumably accidentally, and did not attack until the slug moved. It took a mouthful of slime and cleaned itself. The slug crawled up over the beetle's thorax and escaped.

Eighteen hours after these observations slugs were alive in only two of the dishes, although these individuals had been attacked the day before. The eight beetles in the dishes where the slugs were missing were killed and their crop contents tested. All had eaten slug tissue, including the beetle which had been deliberately avoiding its slug the previous day. Its crop contents were unusual in that they were compact and sticky, adhering to the gut wall. The beetle which had shown no interest in its slug had eventually eaten it and had a very full crop. Another beetle had eaten the slug's soft tissues and left the shell.

In the final trial three F. madida were left overnight with two slugs each, and then their crop contents were tested. Two had full crops and had eaten slugs, while one which had seemed to be moving abnormally had not. Another beetle was kept overnight with one 'sickly' A. reticulatus and ate small parts of it.

These trials indicated that during the day at least F. madida adults are attracted to slugs by movement. When they first attack they are usually repelled by the slime and retreat to clean themselves. In the first two trials only one out of twenty attacked successfully the first time, and it bit the slug half way along its body, in a manner similar to that of Carabus adults. As most of the beetles ate slugs when they were kept together in a confined space it is possible that they could attack them successfully when the slug's supply of slime was exhausted, and would attack them when they were hungry with no choice of food, and when there was no chance of the slug escaping. Darkness is also probably important.

Although these observations were only subjective it was felt that the behaviour of the beetles was tentative compared with that of a Carabus adult which, if it decided to feed went direct to the slug and bit it, with little exploratory behaviour. This behaviour and the fact that only 20% of adults caught in the field had eaten slugs suggests that slugs may form only a minor part of F. madida's diet. They may perhaps be eaten only when circumstances are most favourable e.g. when a slug is dead or dying or is 'cornered'.

Feronia nigra

During 1968 Feronia nigra was trapped only at the Field site, in July and August. Twenty-nine catches were recorded, the first on July 5 and the last on August 30, with a peak about August 1. (Table 14).

In 1969 twenty-one individuals were caught both by pitfall trapping (10) and by hand collection (11) at various sites, other than the original '68 sites. Table 15 shows that most beetles were caught in July. This increase is probably due both to more beetles being active then and also to the fact that traps were set in the potato field only in the last half of June and in July. The 1968 trapping results could have been caused by the beetles moving out into the grass from the neighbouring wood in the summer months when the food supply there would be abundant.

Of the twenty crop contents tested serologically (in 1969) seven (35%) reacted positively, eleven negatively, one crop was empty and the remaining sample gave inconclusive results. (Table 15).

As Greenslade (1963) did not trap F. nigra until April in the South of England and reported that the species overwintered as adults it is possible that the negative March and April individuals, which were found under stones in a wood clearing were hibernating. The March one had a full crop, but most of the contents appeared to be earth.

Although the four May individuals had not eaten slugs they had been feeding, so had left their winter quarters and become active. As the beetle trapped at the Spruce Wood site (Table 15) was caught in an area of dry needles with no green ground vegetation one would not expect slugs to have been available as food.

No collections by hand were made in June and no F. nigra were caught in the pitfall traps.

By July the Potato Field site had flowering plants with a strong leaf cover, while the Edge of Spruce Wood and Wood area sites had grass and small plants; all suitable conditions for slugs. Three of the eleven beetles caught in this month were callow, which agrees with the findings of Lindroth (1945-49) and Larsson (1939). One of these gave the 'doubtful' result. Six of the eight remaining individuals reacted positively. One which was collected in the wood had a distended crop containing greeny-black pieces of tissue. These could have been from an Arion ater or from another invertebrate which had eaten slugs, such as a Carabus larva.

The negative results for beetles collected under the Field stones in July and other months are more difficult to explain, although it may merely be a reflection of the low numbers examined (5). As mentioned in the Methods section these stones are at the edge of a grass field only a few feet from the Edge of Spruce Wood site, where positive results were found. There are moist or almost marshy patches which would seem to be suitable places for slugs. (F. nigra caught at this site in the previous August had been positive in pooled samples).

Finally, the crop of the beetle caught in September was almost empty and the October one was empty; perhaps they were nearing hibernation.

Of the sixteen individuals caught during the months when they were definitely active seven or 43% had eaten slugs.

In the laboratory one F. nigra, in July, was confined with two small A. reticulatus (5 - 7.5 mm stretched out), which it ate within an hour, resulting in a distended crop of chewed-up tissue.

Feronia vulgaris

During 1968 Feronia vulgaris was caught in all months from April to November, except in September. The greatest numbers were caught in June and July. A similar distribution was found during trapping in 1969, although adults were caught in September. The seasonal occurrence is similar to that recorded by Greenslade (1965) in England. As in England this species formed a much smaller part of the carabid fauna than was found in France or Germany (Scherney 1960, Chauvin 1967). Table 16 shows that it was commonest at the Hillside site, but that even there it was not numerous. This could be linked with the fact that the ground was grazed, as Boyd (1960) found that the species prefers ungrazed areas.

The crop contents of twenty-three F. vulgaris were tested serologically (Table 17). Eight (35%) reacted positively, ten negatively, three were empty, and one result was inconclusive.

Two small feeding trials were made. In August '68 one beetle was confined in a box with two A. reticulatus, which were approximately 7 mm and 10 mm when extended. After two days no slugs were seen in the box, and tests showed that the beetle had eaten slug tissue.

In another experiment three F. vulgaris were confined with one 6-7 mm slug. Two ignored it, but one seized the slug and ran around with it for a short time. It then chewed it, holding it between its forelegs and under its body. These beetles were then confined separately for two days with one small slug each. Two ate their slugs and one remained unfed.

It is seen therefore that F. vulgaris is not a very abundant species in the area under study, and that it can eat slugs.

Feronia spp.

Fifteen small Feronia adults were trapped in 1968 from March to August. Because they were examined alive in the field it was not possible to identify their species with certainty, but it was thought that examples of F. diligens, F. nigrita and F. strenua were caught.

In 1969 one F. adstricta, six F. anthracina, one F. diligens, two F. nigrita and fifteen F. strenua were caught and examined serologically. (Tables 18-22). Of these only one beetle, a F. anthracina caught by hand in the spruce wood in October, proved positive.

The single F. diligens caught in June gave a doubtful result when first tested, then a negative one when the test was repeated. Although its crop was quite full the volume of contents extracted was small, because of the beetle's small size (5 mm), so the limits of sensitivity of the test may have been reached and the beetle might have eaten slug tissue.

Twelve of the fifteen F. strenua were found under a stone in March with almost empty crops, and probably were hibernating before emerging later in the spring (Dawson 1965).

Feronia spp. larvae

Table 23 shows the occurrence of Feronia spp. larvae at the different sites during the year March '68 / March '69. At the Hillside site larvae were found in March, April, and October to February; at the Lower Hillside from March to May and October to December; in the Field in November, February and March; in the Spruce Wood in December, February and March; and finally in the

Mixed Hardwood in March to May, September to December and again in March. The species of these larvae was not identified but from Greenslade (1965) and the fact that F. madida was the dominant Feronia species in the area they probably were mostly F. madida, with a few F. vulgaris in the winter months.

The comparatively low numbers trapped agreed with Greenslade's comments on their being caught only infrequently. He caught them in soil and litter and it would seem that these larvae are usually subterranean in behaviour only coming to the surface occasionally. They are not strongly chitinised and are light coloured, a further indication of this type of behaviour.

In 1969 fifteen larvae were tested, three in March, eleven in May, and one in June. (Table 24). Two separate individuals in May were positive as was one pooled sample of two. Thus three or four out of fifteen, or 20-27%, had eaten slugs. (One cannot be certain that both contents in the pooled sample were positive). The following table shows the approximate length of each larva. One can see that they were mostly well developed and would probably be able to attack a small slug successfully. There is however the possibility that the 'positive' larvae could have been scavenging dead slugs.

Length(mm)	17	18	18	18	19	19	21	21	22	23	23	24	24	25	25
+/-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	

The 'positive' larva caught at the Hillside site in May had green gut contents.

TABLE 12

Feronia madida

(1968 trapping: actual and adjusted numbers)

	Hillside	Lower Hillside	Spruce	Field	Mixed Hardwood
March	7 (2.2)	5 (4.1)	0	0	0
April	16 (4.3)	11 (7.8)	0	0	4 (3.5)
May	19 (6.6)	15 (12.0)	0	0	18 (19.3)
June	33 (8.9)	29 (19.7)	2 (1.9)	1 (1.0)	71 (58.9)
July	29 (10.7)	33 (29.7)	0	3 (3.9)	62 (78.1)
Aug.	40 (10.4)	30 (20.1)	3 (3.0)	23 (21.4)	240 (199.2)
Sept.	2 (0.7)	9 (8.0)	0	1 (1.2)	44 (56.3)
Oct.	8 (2.1)	10 (6.7)	0	1 (0.9)	52 (51.5)
Nov.	1 (0.3)	2 (1.5)	0	0	0
Total	155 (46.3)	144 (109.6)	5 (4.9)	29 (28.4)	491 (466.8)

TABLE 13

Feronia madida

(Serological tests: all sites)

	+	-	?	e	N
March	-	-	2	-	2
April	-	4	-	1	5
May	16	26	14	-	56
June	21	77	7	4	109
July	7	44	5	3	59
Aug.	17	71	2	2	92
Sept.	4	17	1	2	24
Oct.	11	24	1	5	41
	76	263	32	17	388

TABLE 14

<u>Feronia nigra</u>

(1968 trapping: actual and adjusted numbers)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
July	0	0	0	8 (10.4)	0
Aug.	0	0	0	21 (19.5)	0

TABLE 15

<u>Feronia nigra</u>

(Serological tests)

	Spruce Wood site		Spruce Wood area			Edge of Spruce wood		Field (stones)		Potato field			Mixed hard-wood area	
	+	–	+	–	e	+	–	+	–	+	–	e	+	–
1968 Aug.	–	–	–	–	–	–	1	*13	–	–	–	–	–	–
1969 March	–	–	–	1	–	–	–	–	–	–	–	–	–	–
April	–	–	–	1	–	–	–	–	–	–	–	–	–	–
May	–	1	–	–	–	–	–	–	2	–	–	–	–	1
June	–	–	–	–	–	–	–	–	–	–	–	–	–	–
July	–	–	1	–	–	2	1	–	2	3	1	1	–	–
Aug.	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Sept.	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Oct.	–	–	–	–	1	–	–	–	–	–	–	–	–	–

* includes pooled samples

TABLE 16

Feronia vulgaris

(1968 trapping: actual and adjusted numbers)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
April	7 (1.9)	1 (0.7)	0	0	0
May	18 (6.3)	0	0	0	0
June	27 (7.3)	4 (2.7)	0	0	0
July	23 (8.5)	0	0	1 (1.3)	0
Aug.	13 (3.4)	0	0	4 (3.7)	1 (0.8)
Sept.	0	0	0	0	0
Oct.	0	0	0	1 (0.9)	0
Nov.	1 (0.3)	0	0	0	0

TABLE 17

Feronia vulgaris

(Serological tests)

	Hillside			Lower Hillside		Field			Field (stones)		Potato field		Mixed hardwood 1968 site			Mixed hardwood area		
	+	-	e	+	-	+	-	?	+	-	+	-	+	-	e	+	-	e
1968 Aug.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
1969 April	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
May	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	1	-	-
June	-	1	-	-	-	-	-	-	-	-	1	1	-	-	1	-	-	-
July	3	2	2	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-
Aug.	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Sept.	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-

TABLE 18

Feronia adstricta
(Serological tests)

	Edge of spruce wood	
	+	-
June	-	1

TABLE 19

Feronia anthracina
(Serological tests)

	Spruce wood area		Edge of spruce wood		Field (stones)	
	+	-	+	-	+	-
Sept.	-	1	-	-	-	1
Oct.	1	2	-	1	-	-

TABLE 20

Feronia diligens
(Serological test)

	Field site	
	+	-
June	-	1

TABLE 21

Feronia nigrita
(Serological tests)

	Lower Hillside		Field (stones)	
	+	-	+	-
March	-	-	-	1
June	-	1	-	-

TABLE 22

Feronia strenua
(Serological tests)

	Hillside		Field		Field (stones)		Potato field	
	+	-	+	-	+	-	+	-
March	-	-	-	-	-	12	-	-
June	-	1	-	1	-	-	-	1

TABLE 23

Feronia spp. larvae
(1968/69 trapping: actual and adjusted numbers)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
March	14 (4.3)	6 (4.9)	0	0	2 (1.9)
April	14 (3.8)	7 (5.0)	0	0	3 (2.6)
May	0	9 (7.2)	0	0	1 (1.1)
June	0	3 (2.0)	0	0	0
July	0	0	0	0	0
Aug.	0	0	0	0	1 (0.8)
Sept.	0	0	0	0	0
Oct.	4(1.0)	2 (1.3)	0	0	2 (2.0)
Nov.	7 (2.1)	1 (0.8)	0	1 (1.1)	2 (2.2)
Dec.	3 (1.3)	1 (1.1)	1 (1.7)	0	1 (1.7)
Jan.	7 (2.5)	0	0	0	0
Feb.	1 (0.3)	0	3 (3.3)	1 (1.2)	0

TABLE 24

Feronia spp. larvae
(Serological tests)

	Upper Hillside		Hillside		Lower Hillside		Field (stones)		Potato field		Mixed Hardwood 1968 site		leaf litter		area	
	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-
March	-	-	-	-	-	-	-	1	-	-	-	-	-	1	1	-
April	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
May	1	-	1	-	-	1	-	-	*2	1	-	3	-	1	-	1
June	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-

Genus Nebria

Nebria brevicollis

In 1968/69 adult Nebria brevicollis were trapped from March until January, with peak numbers in June and September. (Table 25). This agrees with the observations of Penney (1966) in S.W. Scotland. The decrease in numbers probably due to aestivation noted by earlier workers was found at the Field site but not at the Spruce Wood and Mixed Hardwood sites where the beetles were active throughout the summer. At the Lower Hillside site most beetles were active in June and July and no increase in numbers was found later in the year. The seasonal distribution of the larvae is shown in Table 26. They occurred mainly from October to May.

Nebria brevicollis was very numerous with 735 adults recorded throughout the year. It was thus the second most common adult carabid. (824 Feronia madida were trapped in the same period). Nebria sp. larvae were by far the most common, with 2,365 definite records.

The crop contents of sixty-six adults in 1968 and of 361 adults in 1969 were tested serologically. (Table 27). One sample of eight contents proved positive in the first year while the rest were negative. There is the possibility that some at least of these eight adults had eaten a centipede (while being taken to the laboratory). Another centipede caught at the same time reacted positively, so the beetles could have eaten slugs 'second-hand'.

In 1969 eight contents which had been tested separately were positive, as was one sample of five contents. Omitting this latter sample 2% of the beetles tested had eaten slugs. One of these had a distended crop with very chitinous and purple tinged contents, which again suggests that it had eaten some other invertebrate containing slug tissue.

The intestinal contents of twenty-three Nebria larvae were examined. (Table 27). Because the volume per larva was so small they were tested in pooled samples and two of these reacted positively.

Nebria gyllenhali

Nebria gyllenhali was trapped in the Spruce Wood from June to October with the greatest number (42) in August. (Table 28). It was also caught in the Mixed Hardwood in June and July.

The contents from thirty-seven adults were tested. (Table 29), One individual and one pooled sample of two reacted positively (8%). All three contents contained a large amount of chitin.

Nebria spp.

Feeding trials

One N. brevicollis was placed with a small Agriolimax reticulatus (approximately 5 mm when stretched out) in a Petri dish with damp sawdust and observed for an hour. It did not move or show any interest in the slug. (The beetle could have been adversely affected by the daylight).

Six adults were confined with one newly-hatched slug. Two attacked it but drew back immediately. The following day all that was left of the slug was a slimy patch on the sawdust. The crop of one beetle was half-full of slug tissue and the crops of the five others were empty.

Three Petri dishes were half-filled with damp sawdust and ten N. brevicollis or N. gyllenhali and five or six very small or small A. reticulatus were added to each. One day later all the beetles in one dish were killed and found to have empty crops. In the second dish there were two dead slugs and one in the third. The living slugs were removed and the beetles and dead slugs were left together for two days. After this time the dead slugs were still present and the beetles were killed. All their crops were empty so they had not scavenged. It is not known whether the beetles killed the slugs or whether they died naturally.

In a final trial two more dishes with ten Nebria adults were tested with one slug per dish. After twenty-four hours the crops from seventeen N. brevicollis and two N. gyllenhali were empty. One N. brevicollis was very nearly empty and reacted negatively when tested. This food could have been the remains of a previous meal.

To summarise, in these trials only one out of fifty-seven beetles (2%) ate the slugs offered to them. This one ate the smallest slug used in the experiments, a newly-hatched one. Probably size is important as Penney (1966) showed that Nebria preferred food less than 4 mm long.

In one brief trial one Nebria larva did not react to a living slug, but was undoubtedly affected by the daylight shining during the time it was confined with the slugs.

From the preceding data one sees that the number of adults eating slugs in the field was small, and where they had there was the possibility that they had done so 'second-hand'. The feeding trials indicated that adult Nebria are not able to kill slugs unless they are very small, and that they do not usually scavenge even when they are starving.

The small size of the larval head capsule (2 x 1.5 mm), its finely pointed mandibles and its general behaviour suggest that the larvae are merely scavengers.

TABLE 25

Nebria brevicollis adults

(1968/69 trapping: actual and adjusted numbers)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
March	0	3 (2.5)	10 (11.5)	0	5 (4.9)
April	0	3 (2.1)	8 (8.2)	1 (1.0)	3 (2.6)
May	0	3 (2.4)	6 (6.7)	2 (2.4)	9 (9.6)
June	1 (0.3)	41 (27.9)	15 (14.6)	121 (117.4)	63 (52.3)
July	0	26 (23.4)	10 (13.7)	12 (15.6)	19 (23.9)
Aug.	0	2 (1.3)	33 (32.7)	2 (1.9)	21 (17.4)
Sept.	2 (0.7)	3 (2.7)	80 (106.4)	36 (45.0)	32 (41.0)
Oct.	0	6 (4.0)	40 (63.6)	49 (45.6)	30 (29.7)
Nov.	0	4 (3.0)	4 (4.7)	5 (5.4)	6 (6.7)
Dec.	0	1 (1.1)	10 (16.8)	1 (1.7)	1 (1.7)
Jan.	0	0	4 (4.4)	2 (2.0)	0

TABLE 26

Nebria brevicollis larvae

(1968/69 trapping: actual and adjusted numbers)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
March	10 (3.1)	37 (30.3)	195 (224.2)	129 (144.5)	89 (86.3)
April	0	16 (11.4)	106 (108.1)	266 (266.0)	61 (53.7)
May	0	9 (7.2)	37 (41.1)	62 (73.8)	2 (2.1)
"	*1 (0.4)				*1 (1.1)
June	0	0	6 (5.8)	0	0
"		*1 (0.7)			
July	0	0	0	0	0
Aug.	0	0	0	0	0
Sept.	0	0	8 (10.6)	0	2 (2.6)
"			*2 (2.7)		
Oct.	0	4 (2.6)	43 (68.4)	38 (35.3)	22 (21.8)
"		*2 (1.3)		*3 (2.8)	*6 (5.9)
Nov.	1 (0.3)	32 (24.3)	21 (24.6)	156 (168.5)	41 (45.9)
"		*5 (3.8)	*2 (2.3)	*5 (5.4)	*4 (4.5)
Dec.	0	28 (31.9)	18 (30.2)	168 (285.6)	21 (36.1)
"		*1 (1.1)		*4 (6.8)	*1 (1.7)
Jan.	10 (3.6)	32 (21.8)	42 (46.6)	524 (529.2)	43 (44.3)
"		*1 (0.7)		*1 (1.0)	
Feb.	0	2 (1.5)	52 (57.2)	15 (18.3)	17 (17.7)

* = uncertain identification, probably Nebria sp.

TABLE 27

Nebria brevicollis

(Serological tests)

	Hillside			Lower Hillside			Lower Hill-side area			Spruce Wood			Spruce Wood area			Edge of Spruce Wood			Field (stones)		
	+	-	e	+	-	e	+	-	e	+	-	e	+	-	e	+	-	e	+	-	e
1968																					
Aug.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	29	-	-	9	-
Sept.	-	-	-	-	-	-	-	-	-	-	-	-	-	19	-	-	-	-	-	-	-
1969																					
March	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	*6L	-	-	-	5	-
April	-	-	-	-	-	-	-	-	-	*5	-	-	-	-	-	-	-	-	-	1	-
May	-	-	-	-	-	-	-	-	-	1	-	5	-	3	-	-	1	1	-	2	1
June	1	1	-	-	1	-	-	-	-	1,1L	4	-	-	-	-	-	5	-	-	-	-
July	-	-	-	-	-	-	-	-	-	-	3	-	-	7	3	-	11	3	-	-	-
Aug.	-	-	-	-	-	-	-	-	33	-	2	-	1	18	14	-	1	-	-	-	1
Sept.	-	-	1	-	-	-	-	-	-	-	8	17	-	5	-	-	14	1	-	-	-
Oct.	-	-	3	-	-	-	-	-	-	1	15	8	-	2	4	1	15	8	-	1	-

* = pooled sample (s)   L = larva.

TABLE 27 contd.

	Field				Potato field			Mixed Hard- wood site			Mixed Hardwood area			Mixed Hardwood leaf litter			Litter & grass			Garden		
	+	-	?	e	+	-	e	+	-	e	+	-	e	+	-	e	+	-	e	+	-	e
1968																						
Aug.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sept.	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	*8	-	-
1969																						
March	-	4L	-	-	-	-	-	-	-	-	-	-	-	*12L	-	-	-	10	4	-	-	-
April	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
May	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
June	-	16	1	2	-	2	-	1	14	3	-	-	-	1	26	5	-	7	3	-	-	-
July	-	-	-	-	-	-	2	-	2	1	-	-	-	-	-	-	-	1	-	-	-	-
Aug.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Sept.	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	3	-	1	-	-	-	-
Oct.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	2	-	-	-	-

* = pooled sample (s) L = larva

TABLE 28

Nebria gyllenhali

(1968 trapping: actual and adjusted numbers)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
June	0	0	3 (2.9)	0	4 (3.3)
July	0	0	16 (21.9)	0	8 (10.1)
Aug.	0	0	42 (41.6)	0	0
Sept.	0	0	3 (4.0)	0	0
Oct.	0	0	2 (3.2)	0	0

TABLE 29

Nebria gyllenhali

(Serological tests)

	Spruce Wood			Spruce Wood area			Edge of Spruce Wood			Mixed Hardwood 1968 site			Mixed Hardwood leaf litter		
	+	-	e	+	-	e	+	-	e	+	-	e	+	-	e
April	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
May	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
June	-	5	1	-	-	-	-	-	-	-	2	2	-	-	1
July	*2	4	1	-	-	-	-	1	1	-	-	-	-	5	3
Aug.	-	2	-	-	1	1	1	1	-	-	-	-	-	-	-
Sept.	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-

*= pooled sample

Genus Calathus

Calathus fuscipes

In 1968 only four Calathus fuscipes were trapped: one in October at the Hillside site, and one in June and two in October at the Lower Hillside site. (Table 30). This agrees with the findings of Hussey and Lane (1956) who caught their specimens at similar sites, and also did not catch any at the woodland sites. The species was not as numerous as Boyd (1960) and Greenslade (1965) found in their regions.

In 1968 one C. fuscipes caught in a garden about two miles from the trapping sites was found to have eaten slugs. In 1969 two out of four were also positive, one was negative and one gave a doubtful result. Thus three out of five, or 60%, had eaten slugs. (Table 31).

Calathus melanocephalus

In 1968 164 Calathus melanocephalus were caught at the Hillside site from March to October with a peak in August. (Table 32). One was caught at the Lower Hillside site in September, and two in the Spruce Wood in June. This seasonal distribution is two months earlier than Boyd's findings on Tiree where the season was from May to December, with a peak in September and October. Unlike Hussey and Lane (1956) none were trapped in the hardwood area and the numbers were very much higher.

In 1969 callow beetles were caught in June.

In 1968 forty-three crop contents were tested and proved negative. (Table 33). The following year ten were tested from the Upper Hillside site, and one in June proved positive. Thus for all the C. melanocephalus tested one in fifty-three, or 2%, had eaten slugs.

In a laboratory test in August five newly caught beetles were confined for one day with a small A. reticulatus. Afterwards two of their crops were empty and three were very nearly empty, containing a little yellow fluid. When all these crops were washed out with water and tested the result was negative. So although the beetles presumably were hungry they had not successfully attacked the slug.

Calathus micropterus

Fifteen Calathus micropterus were caught at the Mixed Hardwood site from May to September, with a peak in numbers in July. In the Spruce Wood one was caught in April and two in August. (Table 34). This preference for the mixed wood supports the findings of Hussey and Lane (1956).

Twenty-four adults were tested in 1968 and proved negative. (Table 35). In 1969 thirty adults were examined: one was positive in June, as was a pooled sample of three contents in August. Assuming these three were all the same 7% of the beetles had been eating slugs.

Three freshly caught C. micropterus were confined for one day with a small A. reticulatus. The next day the slug was unharmed, and two of the beetles' crops were empty, and one was nearly so.

Another beetle was confined overnight with a slug which died. It was untouched, and the next day the beetle's crop was empty.

Calathus piceus

During the trapping survey ten adult Calathus piceus were caught at the Mixed Hardwood site from April to August with a peak in June. Two were caught in the Spruce Wood in June and two others in September. One beetle which may have been a C. piceus was caught at the Hillside site in September. (Table 36). Although the numbers trapped were so small it seems that they do not agree very closely with the findings of other workers. Greenslade (1965) found a peak in August, while Hussey and Lane (1956) caught their specimens in the Spruce Wood only. Greenslade also trapped no callow adults but in the area under study two were caught in the wood in May (1969).

Twenty-five adults caught at the different wood sites were tested serologically. (Table 37). Three (12%) were positive.

Four freshly trapped C. piceus were confined in the laboratory for one day with a small A. reticulatus. Next day the slug was still alive and one beetle's crop was almost empty. The other three were half-full of food which subsequently proved not to be slug. It seems that the beetles had been feeding before being used in the experiment which therefore was somewhat inconclusive.

Calathus spp.

To summarise, apart from Calathus melanocephalus on the open hillside none of the species in this genus was very common in the area under study. In the laboratory the beetles only approached the slugs accidentally and showed no interest in attacking them. This behaviour and the low incidence of slug eating in the field suggest that C. melanocephalus, C. micropterus and C. piceus are scavengers which may occasionally eat small slugs when circumstances are favourable. Although only five C. fuscipes were examined the fact that three had eaten slugs and that this species is larger than the others suggest that it may actively predate slugs.

TABLE 30

Calathus fuscipes

(1968 trapping: actual and adjusted numbers)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
June	0	1	0	0	0
July	0	0	0	0	0
Aug.	0	0	0	0	0
Sept.	0	0	0	0	0
Oct.	1	2	0	0	0

TABLE 31

Calathus fuscipes

(Serological tests)

	Upper Hillside		Hillside		Lower Hill-side area			Garden	
	+	-	+	-	+	-	?	+	-
1968 Sept.	-	-	-	-	-	-	-	1	-
1969 June	1	-	-	-	-	-	-	-	-
July	-	-	-	-	-	-	-	-	-
Aug.	-	-	-	1	1	-	1	-	-

TABLE 32

Calathus melanocephalus

(1968 trapping: actual and adjusted numbers)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed
March	2 (o.6)	0	0	0	0
April	3 (0.8)	0	0	0	0
May	1 (0.4)	0	0	0	0
June	28 (7.6)	0	2 (1.9)	0	0
July	35 (13.0)	0	0	0	0
Aug.	67 (17.4)	0	0	0	0
Sept.	24 (8.4)	1 (0.9)	0	0	0
Oct.	4 (1.0)	0	0	0	0

TABLE 33

Calathus melanocephalus

(Serological tests)

	Upper Hillside			Lower Hill-side area	
	+	-	e	+	-
1968					
Aug.	-	-	-	-	43
1969					
June	1	2	1	-	-
July	-	-	-	-	-
Aug.	-	4	-	-	-
Sept.	-	-	-	-	-
Oct.	-	2	-	-	-

TABLE 34

Calathus micropterus

(1968 trapping: actual and adjusted numbers)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
April	0	0	1 (1.1)	0	0
May	0	0	0	0	1 (1.1)
June	0	0	0 0	0	0
July	0	0	0	0	12 (15.1)
Aug.	0	0	2 (2.0)	0	1 (0.8)
Sept.	0	0	0	0	1 (1.3)

TABLE 35

Calathus micropterus

(Serological tests)

	Spruce Wood area		Edge of Spruce Wood		Mixed Hardwood leaf litter			Mixed Hardwood litter & grass			Mixed Hardwood area	
1968	+	-	+	-	+	-	e	+	-	e	+	-
Aug. 1969	-	-	-	2	-	-	-	-	-	-	-	22
April	-	1	-	-	-	-	-	-	-	-	-	-
May	-	2	-	1	-	1	-	-	-	-	-	-
June	-	-	-	-	1	2	-	-	4	1	-	-
July	-	-	-	-	-	3	2	-	3	1	-	-
Aug.	-	1	-	-	*1	1	-	*2	2	-	-	-
Sept.	-	-	-	-	-	-	-	-	-	-	-	-
Oct.	-	-	-	-	-	-	1	-	-	-	-	-

* = 3 contents pooled in one positive sample

TABLE 36

Calathus piceus

(1968 trapping: actual and adjusted numbers)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
April	0	0	0	0	?1 (0.9)
May	0	0	0	0	2 (2.1)
June	0	0	2 (1.9)	0	4 (3.3)
July	0	0	0	0	2 (2.5)
Aug.	0	0	0	0	1 (0.8)
Sept.	?1 (0.4)	0	2 (2.7)	0	0

? = identification uncertain

TABLE 37

Calathus piceus

(Serological tests)

	Spruce Wood		Spruce Wood area		Edge of Spruce Wood		Mixed Hardwood 1968 site			Mixed Hardwood leaf litter		Mixed Hardwood litter & grass		Field (stones)	
	+	-	+	-	+	-	+	-	?	+	-	+	-	+	-
1968 Sept.	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
1969 March	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
April	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
May	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-
June	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-
July	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Aug.	-	1	2	-	-	1	-	-	1	-	-	-	1	-	1
Sept.	-	-	-	7	-	-	-	-	-	-	-	-	-	-	-

Genus Amara

Table 38 shows the number of Amara spp. adults which were trapped in 1968. They were much more common at the Hillside site than at the others, occurring from March to September. This distribution is composed of several different species, which could not be separated in the field. It is similar to that found by Boyd (1960) on Tiree who trapped three species between April and October.

Although Davies (1953) had classified the genus as herbivorous crop contents from twenty-four adults were tested. They were caught in April, May and June. (Table 39). Because the volume of contents per beetle was small many of these were pooled. One sample of four contents reacted positively, fourteen negatively and one sample of six gave a doubtful result.

Unfortunately the 1969 trapping to catch adults for testing in some way missed the peak numbers in the spring, although traps were in use most of this time. Either the peak arrived much earlier than in the previous year, e.g. in the first weeks of March, or quickly built up and fell away in the first fortnight of April when the hill traps were not in use. These suggestions seem unlikely because the weather was cold at this time and few other beetles were active. The traps were in regular use for the rest of the spring and summer with no evidence of an increase in numbers. No explanation can be made for this. It would be interesting to know the percentage of Amara spp. which ate slugs because in April 1968 they accounted for 88 of the 125 adult carabids caught at the Hillside site and thus were an important part of the total population at that time. Also, taking Davies' classification of the species as herbivorous into consideration, examination of more adults might have indicated whether the positive result obtained in April was a true one or whether it could have been due to an error in technique.

TABLE 38

Amara spp.

(1968 trapping: actual and adjusted numbers)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
March	8 (2.8)	0	0	0	0
April	88 (23.8)	0	0	0	0
May	47 (16.4)	0	1 (1.11)	3 (3.6)	0
June	24 (6.5)	0	0	2 (1.9)	0
July	4 (1.5)	0	0	0	0
Aug.	2 (0.5)	1 (0.67)	0	0	0
Sept.	1 (0.4)	0	0	1 (1.2)	0

TABLE 39

Amara spp.

(Serological tests)

	Upper Hillside		Hillside			Field		
	+	-	+	-	?	+	-	?
April	-	-	*4	1	-	-	-	-
May	-	1	-	2	-	-	-	-
June	-	2	-	5	*3	-	3	*3

* = pooled samples. The two ? samples in June were pooled together.

Carabid species not found to have eaten slugs

The crop contents from 9 Agonum mulleri, 40 Clivina fossor, one Harpalus latus, 5 Leistus fulvibarbis, 7 Leistus rufescens, 56 Loricera pilicornis and 28 Patrobus excavatus were tested serologically and found not to contain slug tissue. (One Agonum mulleri gave a 'doubtful' result).

Tables 40 - 50 show the seasonal occurrence and the sites at which the beetles used in the tests were caught.

The seasonal occurrence of Clivina fossor was not recorded during 1968 as the beetles seemed to be attracted to the traps and the holes they were sunk in, and it was felt that their numbers would thus be artificially high, compared with those of other species. Also their size (6 mm) made it seem unlikely that they would be able to attack slugs with any success.

Harpalus latus was not trapped in 1968.

TABLE 40

Agonum mulleri
(1968 trapping)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
April	0	0	0	0	1
May	0	0	0	0	1
June	0	0	0	0	1

TABLE 41

Agonum mulleri

(Serological tests)

	Hillside		Field		Field (stones)	
	-	?	-	?	-	?
March	-	-	-	-	1	-
April	-	-	-	-	1	-
May	-	-	3	-	-	-
June	1	-	2	1	-	-

TABLE 42

Clivina fossor

(Serological tests)

	Field site	Potato field
	-	-
June	7	3
July	-	*30

* = some crops were empty

TABLE 43

Harpalus latus

(Serological test)

	Hillside
	-
June	1

TABLE 44

Leistus spp.

(1968 trapping)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
March	8L	7L	2L	0	1L
April	0	1L	0	0	0
May	0	0	0	0	0
June	1 (ruf.)	0	1 (ruf.)	0	0
July	0	0	0	0	0
Aug.	3 (ruf.)	0	0	0	3 (ruf.)
Sept.	0	0	0	0	0
Oct.	2 (ruf.)	0	0	0	2(ruf.,fulv.)
Nov.	0	0	0	0	2,7L(ruf.,fulv.)
Dec.	1L	0	0	0	1,4L (fulv.)
Jan.	20L	21L	0	1L	13L
Feb.	8L	2L	1L	0	6L

ruf. = L. rufescens adult, fulv. = L. fulvibarbis adult, L = larva

TABLE 45

Leistus fulvibarbis

(Serological tests)

	Spruce Wood area		Edge of Spruce Wood		Mixed Hardwood 1968 site		Mixed Hardwood area	
	-	e	-	e	-	e	-	e
March	-	-	-	-	-	-	1	-
Aug.	2	-	-	-	-	-	-	-
Oct.	-	-	-	1	1	-	-	-

TABLE 46

Leistus rufescens
(Serological tests)

	Potato field		Mixed Hardwood 1968 site		Mixed Hardwood area		Various	
	-	e	-	e	-	e	-	e
1968 Aug.	-	-	-	-	1	-	3	0
1969 June	-	1	1	-	-	-	-	-
July	1	-	-	-	-	-	-	-

TABLE 47

Loricera pilicornis
(1968 trapping)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
April	0	0	1	7	0
May	1	4	0	14	0
June	2	3,5L	2	32,19L	5,?1L
July	1L	4L	2	13,10L	3, 3L
Aug.	4,3L	3,3L	1,?1L	2,9L	0
Sept.	0	1L	1	1,?1L	1,?1L
Oct.	0	? 3L	0	1,2L,?4L	?5L
Nov.	0	? 4L	1L	1,?5L	1,?3L
Dec.	0	? 1L	4L	2,?3L	?1L
Jan.	0	1L,?2L	3L	4,?1L	1L
Feb.	0	0	0	0	?1L

L = larva ?L = uncertain identification

TABLE 48

Loricera pilicornis

(Serological tests)

	Hillside		Spruce Wood		Edge of Spruce wood		Field		Field stones		Potato field	
	-	e	-	e	-	e	-	e	-	e	-	e
1968 Aug.	-	-	-	-	-	-	-	-	5	-	-	-
1969 March	-	-	1	-	-	-	-	-	-	-	-	-
April	-	-	-	-	-	-	1	-	-	-	-	-
May	-	-	-	-	1	-	-	-	-	-	3	-
June	3	-	-	-	2	5	5	2	-	-	1	-
July	-	-	-	-	-	-	-	-	-	-	-	3
Aug.	-	-	-	-	-	-	-	-	-	-	-	-
Sept.	-	-	-	-	1	-	-	-	-	-	-	-
Oct.	-	-	-	-	1	-	-	-	-	-	-	-

	1968 site		Mixed Hardwood litter & grass		area		Various	
	-	e	-	e	-	e	-	e
1968 May	-	-	1	-	-	-	-	-
June	1	-	-	1	-	-	7	11
July	-	-	-	-	-	-	-	-
Aug.	-	-	-	-	-	-	-	-
Sept.	-	-	-	-	-	-	-	-
Oct.	-	-	-	-	-	1	-	-

TABLE 49

Patrobus excavatus

(1968 trapping)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
May	0	0	(1)	0	0
June	0	0	(2)	0	0
July	0	0	4	0	2
Aug.	0	0	38,(1)	0	3
Sept.	0	0	5	1	5
Oct.	0	0	0	0	2

( ) = uncertain identification

TABLE 50

Patrobus excavatus

(Serological tests)

	Spruce Wood		Spruce Wood area		Edge of Spruce Wood		Potato field		Mixed Hard-wood site	
	-	e	-	e	-	e	-	e	-	e
1968 Aug.	-	-	-	-	4	-	-	-	-	-
1969 March	-	-	-	3	-	-	-	-	-	-
April	-	-	-	-	-	-	-	-	-	-
May	-	-	-	-	-	-	-	-	-	-
June	-	1	-	-	1	2	-	-	1	-
July	-	-	4	1	-	-	2	1	-	-
Aug.	1	-	5	-	-	-	-	-	-	-
Sept.	-	-	-	-	-	-	-	-	-	-
Oct.	1	-	1	-	-	-	-	-	-	-

(B) Family Staphylinidae

Staphylinus aenocephalus

During 1968 many staphylinids were caught in the pitfall traps throughout the year. As many of these beetles look similar when examined in the field it was not possible to record the seasonal occurrence of each species, with the exception of Staphylinus aenocephalus which is easily distinguishable. Table 51 shows that it occurred in every month except July and August, with peak numbers in March and November. It was caught at the hillside sites only.

In 1969 eleven S. aenocephalus were tested serologically and eight proved negative. (Table 52). The remaining sample of three reacted positively, (Plate 13), but the beetles had fed on the internal organs of a Cychrus caraboides larva, while being taken to the laboratory, and had thus very probably eaten 'second-hand' slug material.

Philonthus decorus

Fifty Philonthus decorus were trapped and tested serologically. (Table 53). Because each staphylinid had only a small volume of liquid gut contents many of the contents were pooled to form larger samples. Twenty-three individuals were definitely negative, and the samples containing the other twenty-seven reacted positively. Because of the pooling of the contents it was not possible to estimate the percentage which had eaten slugs.

In the laboratory five freshly caught adults were confined together for one day with a small, healthy and active Agriolimax reticulatus and with a weak 'sickly' one. Almost immediately two attacked the sickly slug and appeared to start feeding on it. The following day the active slug was still alive and remains of the sickly one were still in the dish. The five beetles were killed, and on testing, their intestines were found to be full of a red brown liquid which was of slug origin. From these observations it is highly probable that these staphylinids at least are scavengers feeding on dead or dying slugs.

Quedius lateralis

Four Quedius lateralis were tested. (Table 54). The first sample which contained the contents from three from the mixed hardwood region proved positive while the remaining individual from the same area was negative.

Other species

Ten Philonthus carbonarius, five P. intermedius, eight P. laminatus, two Quedius fuliginosus, three Olophrum piceum and one Xantholinus glabratus were tested serologically and were found not to have eaten slugs. (Tables 55-60).

(C) Family Scarabaeidae

Two scarabid adults were caught and found not to have eaten slugs. These were an Aphodius rufipes caught in September at the Hillside site, and a Geotrupes stercorarius caught in April at the Lower Hillside site.

TABLE 51

Staphylinus aenocephalus

(1968 trapping: actual and adjusted numbers)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
March	15 (4.6)	2 (1.6)	0	0	0
April	11 (3.0)	1 (0.7)	0	0	0
May	4 (1.4)	0	0	0	0
June	1 (0.3)	1 (0.7)	0	0	0
July	0	0	0	0	0
Aug.	0	0	0	0	0
Sept.	7 (2.4)	0	0	0	0
Oct.	16 (4.2)	1 (0.7)	0	0	0
Nov.	17 (5.1)	5 (3.8)	0	0	0
Dec.	5 (2.2)	1 (1.1)	0	0	0
Jan.	5 (1.8)	0	0	0	0
Feb.	1 (0.3)	0	0	0	0

TABLE 52

Staphylinus aenocephalus

(Serological tests)

	Upper Hillside		Hillside	
	+	−	+	−
May	−	1	−	−
June	−	−	−	3
July	−	−	−	−
Aug.	−	−	−	−
Sept.	−	−	−	−
Oct.	−	2	*(3)	2

* see text

TABLE 53

Philonthus decorus
(Serological tests)

	Spruce Wood		Field		Mixed Hardwood litter & grass		Mixed Hardwood area	
	+	-	+	-	+	-	+	-
1968								
Aug.	-	-	-	-	-	-	*6	-
1969								
March	-	2	-	-	-	-	-	-
April	-	-	-	-	-	-	-	-
May	-	-	-	-	-	2	-	-
June	-	-	-	1	*19	20	-	-

* = pooled samples

TABLE 54

Quedius lateralis
(Serological tests)

	Mixed Hardwood leaf litter		Mixed Hardwood area	
	+	-	+	-
1968				
Sept.	-	-	*3	-
1969				
Sept.	-	1	-	-

* = pooled sample

TABLE 55

Philonthus carbonarius

(Serological tests)

	Spruce Wood area		Potato field		Mixed Hardwood area	
	+	-	+	-	+	-
1968						
Sept.	-	-	-	-	-	4
1969						
March	-	2	-	-	-	-
April	-	-	-	-	-	-
May	-	-	-	4	-	-

TABLE 56

Philonthus intermedius

(Serological tests)

	Potato field		Field	
	+	-	+	-
May	-	2	-	-
June	-	-	-	3

TABLE 57

Philonthus laminatus

(Serological tests)

	Field		Field (stones)	
	+	-	+	-
March	-	-	-	4
April	-	-	-	-
May	-	1	-	-
June	-	3	-	-

TABLE 58

Quedius fuliginosus

(Serological tests)

	Hillside
	-
June	1
Oct.	1

TABLE 59

Olophrum piceum

(Serological tests)

	Mixed hardwood area
	-
March	3

TABLE 60

Xantholinus glabratus
(Serological test)

	Hillside
	-
Oct.	1

(D) Family Silphidae

Phosphuga atrata

Seasonal occurrence

In 1968 two adult Phosphuga atrata were trapped at the Mixed Hardwood site in June and one in July. One silphid larva (which probably was of this species) was caught in June at the same site, and another in August. (Table 61). Hussey and Lane (1956) had caught their one specimen at their hillside site and gave no indication of the month when it was trapped.

In 1969 callow and mature adults were found in May and June, and only mature adults in July and October. A larva was caught in August.

Serological Tests

In August 1968 one adult was trapped near the Mixed Hardwood site and was found not to have eaten slugs. Another caught in the marsh near the Hillside site had. (Table 62).

In 1969 thirteen adults were tested, nine from the three sites in the Mixed Hardwood area, one from under stones near the edge of the Spruce wood, two from the Hillside site and one from the Upper Hillside site. (Table 62). Only one from the Mixed Hardwood clearing with grass and leaf litter was positive. Thus only two out of the fifteen (13%) reacted positively.

It was thought that three of four large silphid larvae examined, (two in August 1968 and one in August 1969) were young Phosphuga. One of these reacted positively when tested. (Table 63).

Discussion

The low percentage of positive results for a species which reputedly eats molluscs could be influenced by various factors: Firstly, the beetles could have been feeding on non-molluscan food, but the description given by Linssen (1959) shows that their mode of feeding is highly specialised so this seems unlikely. Secondly, because of this specialisation the beetles would perhaps normally only feed on snails (which retract into their shells when disturbed) and would be unable to attack the more active slugs successfully. However, very few snails were observed in the area under study, and it is uncertain whether there would be enough present to be the only source of food.

Thirdly, there is the possibility of a fault in technique with insufficient fluid being extracted from the beetles for the test to react successfully. In contradiction of this is a note concerning the 1969 positive sample which mentions that 'only a little fluid' was extracted from the beetle's abdomen.

Finally, but perhaps most important, Linssen describes how the beetle eats its way through a snail's slime and tissues with the aid of a secretion which has a solvent action. The fluid extracted from the beetles was of the same brown colour which in other species such as Cychrus is often associated with 'liquefied' slug, but it reacted negatively in the tests. Perhaps this secretion changes the structure of the tissues so radically that their antigenic properties are altered and the antibody - antigen reactions cannot take place. There is therefore scope here for further investigation.

TABLE 61

Phosphuga atrata
(1968 trapping)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
June	0	0	0	0	1,1L
July	0	0	0	0	1
Aug.	0	0	0	0	1L

L = silphid larva (?Phosphuga atrata)

TABLE 62

Phosphuga atrata (adults)
(Serological tests)

	Upper Hillside		Hillside		Hillside Marsh		Field (stones)		Mixed Hardwood 1968 site		leaf litter		litter & grass	
	+	−	+	−	+	−	+	−	+	−	+	−	+	−
1968														
Aug.	−	−	−	−	−	−	−	−	−	−	0	1	−	−
Sept.	−	−	−	−	1	0	−	−	−	−	−	−	−	−
1969														
May	−	−	−	−	−	−	0	1	−	−	−	−	0	1
June	−	−	0	2	−	−	−	−	0	1	−	−	1	4
July	−	−	−	−	−	−	−	−	−	−	0	1	0	1
Aug.	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Sept.	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Oct.	0	1	−	−	−	−	−	−	−	−	−	−	−	−

TABLE 63

Silphid larvae (?Phosphuga atrata)
(Serological tests)

	Hillside Marsh		Edge of Spruce Wood	
	+	−	+	−
1968 Aug.	0	1	0	1
1969 Aug.	1	0	−	−

(E) Other species

At various times a few other types of invertebrate were tested serologically.

Cantharidae (Coleoptera)

One cantharid larva caught in March 1969 at the Field site produced a positive reaction when tested serologically. Table 64 shows the seasonal distribution of such cantharid larvae during 1968/69. Only two adults were caught, presumably because the adult beetles can fly and thus escape from the traps. Further tests, would have to be carried out before any conclusions about the significance of these larvae are drawn, but their comparatively small size and structure in general suggest that they may be scavengers.

Earwig (Dermaptera)

An earwig trapped at the Upper Hillside site in August had not eaten slugs.

Harvestmen (Phalangida)

In August 1968 a pooled sample of twenty-five unidentified harvestmen from the mixed hardwood area reacted positively. Five more caught in the same region in August of the following year were negative, as was one caught in the spruce wood. Two from the hardwood area in September gave a doubtful result, while in October two at the Upper Hillside site were negative and another gave a doubtful result. One trapped, in the latter month, at the Lower Hillside site was positive.

No records were kept of the harvestmen caught during the trapping survey, mainly because the larger ones (like those tested) were able to crawl out of the small traps.

The 'doubtful' results highlight one of the difficulties encountered when one tests contents from invertebrates other than carabids. The carabid's large distendable crop makes extraction of contents comparatively simple, but in animals such as harvestmen the gut is diverticulated and extraction is difficult. In the present work the abdomens were squashed and fluid pipetted out of them. This of course resulted in more than gut contents being extracted.

Plate 12 shows the results obtained with the first sample recorded as positive. One can see that distinct lines have developed as well as a diffuse area. Plate 13 shows the other positive result. (The sample was in the top left well). Here again a definite line has formed in front of the well, but there is also a diffuse patch encircling it, and another in front of the central well. In the 'doubtful' sample a similar diffuse area formed round the well but there were no definite lines. It is difficult to interpret these results without further experimentation but it is possible that the diffuse areas round the wells containing the samples to be tested were caused by the actual diffusion of material outwards and not by precipitation formed by the antibody/antigen reaction. If extensive tests were going to be made of extracts from harvestmen one would have to develop a technique for filtering and clarifying these before testing them. Only then could one be certain that the interpretation of the reactions in the plates was correct.

<u>Centipedes</u> (Chilopoda)

In September 1968 fifteen lithobiomorph centipedes caught in a garden two miles from the trapping sites reacted negatively. One geophilomorph centipede caught at the same time reacted positively. Three unidentified centipedes

PLATE 12

1. Harvestmen 2. A. reticulatus

4. A. reticulatus 3. Harvestmen

PLATE 13

1. Harvestmen 2. Carabus larva (negative)

4. A. reticulatus 3. Staphylinus aenocephalus

caught the following March in a greenhouse had not eaten slugs although there were a few slugs near them when they were caught. (The structure of the group is such that the gut could not be pulled out, so once again abdominal contents were tested.)

In the laboratory one large lithobiomorph was confined for a short time with a small Agriolimax reticulatus. As soon as it touched the slug it retreated and cleaned itself thoroughly, drawing all its legs and appendages through its mouthparts. It did not go near the slug again, and the experiment was stopped.

During the regular trapping centipedes were never found in the traps, although millipedes were occasionally, so their seasonal occurrence and importance is unknown as far as this study is concerned.

TABLE 64

Unidentified cantharid larvae

(1968 trapping: actual and adjusted numbers)

	Hillside	Lower Hillside	Spruce Wood	Field	Mixed Hardwood
March	9 (2.8)	6 (4.9)	2 (2.3)	3 (3.3)	1 (1.0)
April	6 (1.6)	1 (0.7)	0	0	0
May	0	0	0	0	0
June	0	0	0	0	0
July	1 adult	1 adult	0	0	0
Aug.	0	0	0	0	0
Sept.	0	1 (0.9)	0	0	0
Oct.	0	0	0	2 (1.9)	0
Nov.	0	1 (0.8)	0	3 (3.2)	0
Dec.	6 (2.6)	0	0	3 (5.1)	0
Jan.	4 (1.4)	1 (0.7)	0	3 (3.0)	0
Feb.	2 (0.6)	0	0	0	0

DISCUSSION AND CONCLUSIONS

Most of this section will be confined to a discussion of the role of carabids in the predation of slugs, as this group was studied in the most detail.

(A) Feeding trials v. serological tests

In the preliminary feeding trials (Page 6) the species tested were arranged in an order of preference for eating slugs which was different from that subsequently found by examination of the crop contents of beetles fresh from the field. The following table shows this:

	Trials		Crop contents
1.	F. nigra	1.	C. caraboides
2.	C. caraboides	2.	C. catenulatus
3.	F. vulgaris	3.	F. nigra
4.	N. brevicollis	4.	F. vulgaris
5.	F. madida	5.	F. madida
6.	? C. catenulatus	6.	N. brevicollis

The most notable difference is the position of Carabus catenulatus. 67% at least of those tested serologically had eaten slugs while it was doubtful whether the three tested in the feeding trials for several weeks ate any. Although no C. catenulatus were used in the small feeding trials made later one newly trapped C. violaceus ate a slug quickly and efficiently. This discrepancy could have been caused by individual feeding preferences: in the first trials the beetles were kept in the laboratory for several weeks both to acclimatise them to the new conditions, if possible, and to ensure that they were healthy. During this time they were fed with a continuous supply of tinned dog food. There is the possibility that during this time they became accustomed to this type of food and when confronted with living prey, which possibly was rather too large, they were disinclined to attack it.

Individual differences in the 'willingness' to eat slugs had been noticed in the feeding trials with F. nigra and F. vulgaris, where it appeared that if a beetle once started to feed on slugs it would continue to do so, but if it never started it might starve even in the presence of slugs. These trials also indicated that if some species, e.g. F. nigra, were fed exclusively with slugs they might die sooner than if they had had a more varied diet. This could be due to deficiencies in the diet but the deaths might also have been caused by other factors such as disease, the higher temperatures in the laboratory, and the possibility that the individuals tested were nearing the end of their lives anyway.

To revert to the table, the relative positions of F. nigra and C. caraboides are reversed because the positions of the beetles in the trials column was derived, as described above, from the length of time the slugs survived in the cultures. Although in the field more individual C. caraboides had been eating slugs, in the laboratory they ate less and at a slower rate than F. nigra; so their slugs lived longer.

The position of N. brevicollis before F. madida in the preliminary trials was almost certainly the result of the artificially confined experimental conditions and the absence of a choice of food. It should be noted that in the later trials (Pages 65-67 and 81) more F. madida ate slugs than did N. brevicollis. The discrepancy cannot be explained with certainty but is probably the result of the improved conditions in the second series of trials.

The results obtained from the serological tests thus supported the feelings of uncertainty concerning the usefulness and reliability of simple feeding trials which were felt during the introductory studies.

(B) Beetle size and the percentage of predation

It was considered that a relationship existed between the predation percentage and the size of the predators. Table 65 shows the different carabid species, arranged in order of size, the number of each tested serologically, and the percentage of beetles which had eaten slugs. The percentage is only approximate because in many cases it has been calculated from numbers smaller than 100, and also, it only takes into account samples which were definitely positive, ignoring 'doubtful' ones.

Table 65 shows that the percentage of individuals per species which had eaten slugs is greater in the larger beetles, and that most of the smaller ones had not eaten any. This impression was confirmed statistically when the correlation coefficient for median size and the corresponding percentages was calculated and found to be very significant. ($r = 0.897$ $P\ 0.1 = 0.652$).

This correlation is almost certainly due to the fact that the larger beetles are more capable of killing slugs than the smaller ones because of their larger size, greater strength and strongly developed mouthparts. Unlike the smaller species they can hold the slugs firmly in their mouthparts, clear of the rest of their head, and thus do not become smeared with slime. The largest beetles, such as the *Carabus* species, are strong enough to cut the slugs in two and are thus able to eat them immediately, while the smaller ones have to struggle with the slugs and may only occasionally succeed in killing them.

TABLE 65

Species	Size (mm)	Number tested	% positive
Carabus violaceus	24	9	100
Carabus catenulatus	20 - 24	16	67
Carabus nemoralis	20 - 24	7	71
Feronia nigra	18 - 20	34	43
(Carabus arvensis)	16 - 20	(1)	*
Feronia vulgaris	15 - 17	23	35
Cychrus caraboides	16	23	73
Feronia madida	14 - 16	509	20
Calathus fuscipes	9 - 12	5	60
Nebria brevicollis	9 - 12	427	2
Feronia anthracina	9 - 11	6	17
Feronia adstricta	10	1	0
Feronia nigrita	8 - 11	2	0
Calathus piceus	8 - 10	25	12
Nebria gyllenhali	8.5-9.5	37	8
Harpalus excavatus	8 - 9	1	0
Loricera pilicornis	7 - 8**	56	0
Patrobus excavatus	7 - 8	28	0
Calathus micropterus	7	54	7
Leistus fulvibarbis	6.5-7.5	5	0
Agonum mulleri	6 - 8	9	0
Calathus melanocephalus	6 - 7	53	2
Leistus rufescens	6	7	0
Clivina fossor	6	40	0
Feronia strenua	5.5	15	0
Feronia diligens	5	1	0

* ate slugs in the laboratory

Size from Fowler (1887-91), except ** from Joy (1932)

(C) Analysis of results of Feronia madida serological tests

Feronia madida is the only species which regularly eats slugs in which enough individuals were tested serologically to enable an analysis to be made of results obtained over a period of months.

Seasonal changes

In an attempt to discover whether there was a seasonal change in the percentage of F. madida which had eaten slugs, chi-square tests were made, according to the methods given in Bailey (1959), to compare the ratios of the number of positive samples to the remaining ones (i.e. negative, doubtful and empty) per month. (Table 13, Page 73). No significant difference was found during the period May to October. (X^2 = 7.71 P 5 = 11.07). There were too few samples in March and April for statistical analysis.

This result is to some extent misleading and is due to the combining of the last three categories together. If one tests the ratio of 'positive and doubtful / 'negative and empty' from May to October the result shows a very significant difference. (X^2 = 24.78 P 0.1 = 20.51). If however one excludes the May sample the chi-square is not significant. (X^2 = 2.15 P 5 = 9.49). An inspection of Table 13 shows that the ratio of 'doubtful' / 'the rest' for May is larger than usual, and it is significantly different when compared with that for the remaining months combined, (X^2 = 23.85 P 0.1 = 13.82). Thus in May the number of doubtful results, which could have been either positive or negative, and which were obtained before the technique was finalised, influenced the results.

Another way of comparing the monthly results which makes comparisons with other species easier is to calculate the percentage of beetles which had eaten slugs per month. (Table 66). These values, for May to October, ranged from 12% to 29% with a mean of approximately 20%. As these were not significantly different, ($X^2 = 3.64$ P 5 = 11.07), there was a confirmation that no obvious seasonal trend had occurred. However, although the percentage of predation remains around 20% throughout the months the adult beetles are active, pitfall trapping suggests that the number of beetles in the field rises, as the season progresses, to an August peak and falls from then until November. To maintain the percentage of predation the number of beetles actually eating slugs must vary throughout the season with more doing so in August than in the earlier and later months.

TABLE 66

Feronia madida

(serological tests: all sites)

	+	N	% +
March	0	2	0
April	0	5	0
May	16	56	29
June	21	109	19
July	7	59	12
Aug.	17	92	18
Sept.	4	24	17
Oct.	11	41	27

The amount of food needed to maintain the level will, obviously, also have to rise and fall. Warley (unpublished) made monthly counts of the numbers of slugs occurring in turf about ½ mile from the Mixed Hardwood site. He found that the numbers of newly-hatched Agriolimax reticulatus rose from almost nil in June to a peak in August, with a decline in September and a steady drop in October and November. Another small peak of newly-hatched slugs occurred in December. Arion hortensis and A. fasciatus had similar peaks in August, but neither had the secondary peak in December. A. hortensis had another peak in October. It can be seen that at the time (August) when, theoretically, there are the most predators around, slugs are most numerous in their most vulnerable stage. Some of the newly-hatched A. hortensis in October could be eaten but the young A. reticulatus in December would escape predation by adult F. madida.

Although no seasonal changes were found it is probable that the nutritional requirements of the beetles would in fact vary at the time of breeding (July and August) when slugs could be a convenient source of a large amount of protein.

Nocturnal/diurnal behaviour

If the nocturnal activity of F. madida in woodland and its diurnal activity in grassland (Williams 1959b) are strongly developed in the area under investigation one could expect the percentage of beetles eating slugs in wooded areas to be higher than in grassland, slugs also being more active nocturnally. The different sites were therefore divided into two groups (1) those in wooded areas and (2) those in more open or grassy areas. (Tables 67 and 68). In both groups the percentage of beetles which had definitely eaten slugs is similar, 18% in wooded and 24% in open areas. If the ratio of 'positive'/ negative or empty'/'doubtful' samples for the two groups of sites are compared statistically it is found that there is no significant difference between them. (X^2 = 1.94 P 5 = 5.99).

Thus, if the differences in behaviour do occur they do not appear to be reflected in the percentage of the populations eating slugs. This theory of course assumes that slugs are equally available in both groups of habitats. If the absolute numbers of slugs and beetles could be determined it might be found that, comparatively speaking, a higher percentage of the slug population in one type of habitat was eaten than in the other.

TABLE 67

Feronia madida
(wooded areas)

	+	-	?	e	N
Spruce Wood site	1	1	-	-	2
Spruce wood area	1	1	2	-	4
Edge of Spruce wood	-	3	1	-	4
Mixed Hardwood					
" 1968 site	7	22	1	-	30
" leaf litter	23	71	8	5	107
" litter & grass	21	105	13	7	146
" area	-	1	-	-	1
	53	204	25	12	294
%	18	69	9	4	

TABLE 68

Feronia madida

(open areas)

	+	–	?	e	N
Upper Hillside	6	17	1	–	24
Hillside site	3	13	–	2	18
Hillside area	–	1	–	–	1
Lower Hillside site	2	10	2	1	15
Lower Hillside area	3	–	2	–	5
Field site	1	1	–	1	3
Field (stones)	3	9	1	1	14
Potato field	3	8	–	–	11
Field or mixed hardwood	2	–	1	–	3
	23	59	7	5	94
%	24	63	8	5	

Percentage predation and crop distension

The state of distension of the crops was originally recorded to aid in the interpretation of the results of the serological tests, e.g. if a crop was almost empty a negative reaction could be the result of there being too little food present to react, while if it were full the same result would mean that some other food had been eaten.

About 21% of the crops were unclassified due to changes in technique and resulting from the pressure of work involved in removing the crop contents from a large number of beetles at the peak of the season in the shortest possible time, before they were digested. As will be shown later it is possible that many of these unclassified crops were full of food.

In Table 69 the 'state as percentage of total' values show that the crops were found in a broad spectrum of states from empty to greatly distended (a state in which the crop was so distended it must have filled most of the abdomen, pressing many of the organs aside). From the state of their crops it was obvious that the majority of the beetles had been feeding. This may reflect the fact that most were caught in pitfall traps and thus had been active and were in a situation where they could have caught food. (The lower value for the state between half full and full is probably due to a bias in estimating the volume of the contents visually).

From the 'percentage composition of all the positive samples' it can be seen that most positive samples (i.e. those containing slug material) were derived from full or distended crops.

From the 'percentage positive in each individual state' it can be seen that the fuller the crop the more likely it is to contain slug tissue, with a steady rise from the 3% for the less than half full crops to the 71% of the greatly distended. A comparison of the 26% for the unclassified with the 28% for the full crops suggests that many of the former were full.

The fact that the fuller crops are more likely to contain slug material is probably due to the fact that one slug provides a larger supply of food than any other food with the exception of an earthworm, so that when the beetle has killed it, it has more of an opportunity to stuff its crop full than if it were moving around catching small insects or larvae. Conversely, it also means that the beetle will kill fewer slugs in order to satisfy its nutritional requirements than if the slug were a smaller animal.

TABLE 69

Feronia madida

(State of crop distension)

State of crop	+	–	?	N	State as % of total	% + of total +	% of state positive
empty	–	–	–	17	4	0	0
almost empty	2	18	4	24	6	3	8
less than half full	2	56	3	61	16	3	3
half full	4	55	4	63	16	5	6
more than half full	5	29	0	34	9	7	15
full	17	42	1	60	15	22	28
distended	15	17	1	33	9	20	45
greatly distended	10	4	0	14	4	13	71
unclassified	21	42	19	82	21	27	26

(D) The significance of predation by adult carabids

In an attempt to assess the significance of predation by adult carabids estimates were made of the possible number of beetles trapped in 1968/69 which could have eaten slugs. These were calculated using the approximate percentages of beetles in each species which were found during the serological tests to have eaten slugs.

These estimates were limited to adult carabids because they were easily recognisable as such in the field and had been subject to the most intensive serological study. Because of the uncertain importance of Amara, as noted above, this genus was excluded from the calculations. Carabid larvae were not included because the smaller ones were less easily distinguishable in the field from staphylinids, for example, and the percentage of Nebria larvae eating material of slug origin was uncertain.

The estimates of numbers of possible predators were calculated as follows. First, the total number of all species of carabids caught during the trapping survey was extracted from the field records. (The adjusted values of numbers per 287 traps per month were used throughout). Secondly, the numbers of each species discovered later to be capable of eating slugs were separated from these. Finally, using the percentages found in the serological testing an estimate was made for each species of how many might have eaten slugs. (Table 70). The estimates were made for each month, so that with e.g. F. madida where the percentage eating slugs was found to be about 20% and where 122 were caught at all the sites in July, 20% of these, or 24, could have eaten slugs.

Figure 4 shows the distribution of carabid adults at all the sites throughout the year and the numbers which could possibly have eaten slugs. The most noticeable point is that over the year only 9% of all the adults caught would be involved. This low value is strongly influenced by the low percentage of predation in the two dominant species, Feronia madida (20%) and Nebria brevicollis (2%).

Another point is that although only 20% of F. madida (or 28% at the most if all the doubtful results in the serological tests were included) might be eating slugs the large number of this species compared with other species weights the figures heavily. It theoretically makes up 61% of all carabid predators, and so is more important in the overall predator/prey relationships than its predation rate suggests. Conversely, the large Carabus species, with a predation rate of 67% to 100% account for only 12% so their importance may be less than it appears at first glance. It should be remembered, however, that because of their size the Carabus species might be able to eat as much individually as several Feronia.

The data from the Mixed Hardwood, Lower Hillside and Field sites give contrasting examples of the various relationships which can exist between F. madida and the other species and their relative importance in the theoretical number of predators.

The Mixed Hardwood site yielded the greatest number of F. madida - 54% of the total adult carabids caught, and 87% of the theoretical number of predators. Figure 5 and Table 71 show that from August to November this species could contribute most of the slug eaters, while in June and July its numbers would be swollen by other genera such as Carabus, Nebria and Calathus. 12% of the adults caught at this site could be involved in predation.

At the Lower Hillside site F. madida made up 46% of the total adult carabid catch, and 71% of the theoretical number of predators. In a similar way to the previous site it could make up most of the slug-eating population from July to November, but from April to June other species could play almost as important a part e.g. Carabus spp. and F. vulgaris. (Figure 6 and Table 72). 13% of the adults caught could have been involved in predation.

Finally, at the Field site where F. madida was least common, 5% of the total adult catch, it accounted for 21% of the possible predators. (Figure 7 and Table 73). Only 4% of all the adults were theoretically likely to have been acting as predators. This is partly due to the low incidence of

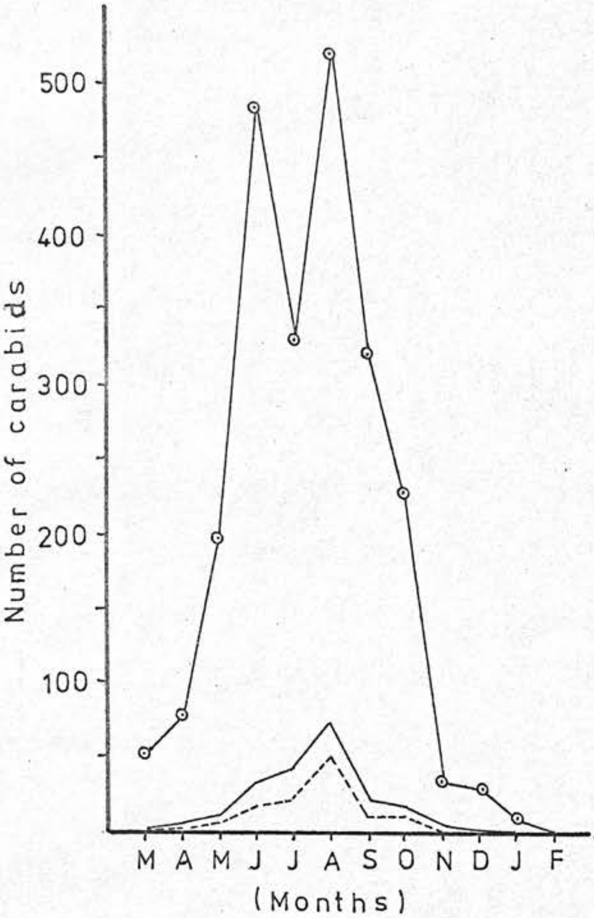

Figure 4: All sites

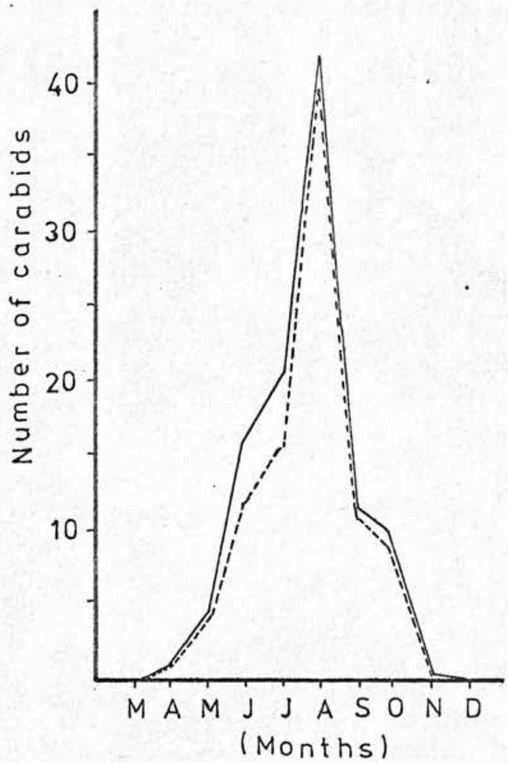

Figure 5: Mixed Hardwood

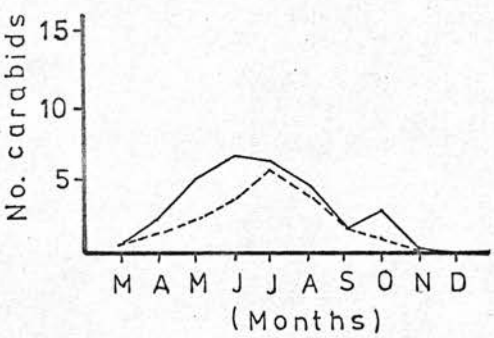

Figure 6: Lower Hillside

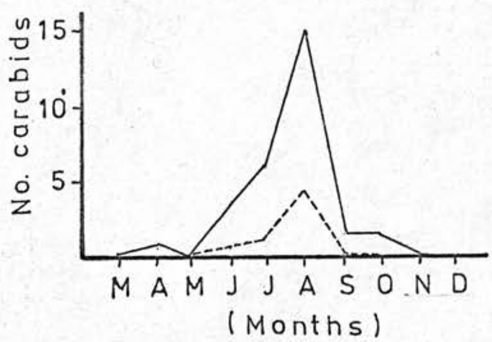

Figure 7: Field

Figures 4 - 7: o—o = number trapped 1968/69. ——— = theoretical no. predators. ----- = theoretical no. *F. madida*.

F. madida at this grassy site and partly to the higher numbers of small species such as Loricera pilicornis which do not eat slugs. Figure 7 shows that, as at the other sites, F. madida was commonest in August, but even then it only accounted for 29% of the population. The balance was made up mainly by the sudden increase in F. nigra and F. vulgaris.

The above discussion only concerns adult carabids and their numbers would be augmented throughout the year by Carabus spp. and/or Feronia spp. larvae, which can eat slugs. As mentioned above, Nebria sp. larvae were very much the most numerous coleopteran (2,586 when standardised) and the effect of this large number on slug populations is uncertain, but as they are most probably mainly scavengers they may not directly affect the numbers of living slugs.

TABLE 70

	Total carabid adults trapped	No. individuals of predaceous species	Theoretical No. of predators	Theoretical No. F. madida	Percentage predators
March	55	26	2	1	4
April	80	38	7	3	9
May	199	72	13	8	7
June	484	342	33	18	7
July	330	288	43	24	13
August	521	408	75	51	14
September	321	284	21	13	7
October	227	213	18	12	8
November	32	22	1	<1	3
December	27	21	<1	0	1
January	8	6	<1	0	1
February	0	0	0	0	0
Total	2284	1720	214	130	9

TABLE 71

Theoretical numbers of predators in 1968/69 catch.

	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Mixed Hardwood										
<u>C. catenulatus</u>	-	-	-	-	-	1.1	-	-	-	-
<u>C. nemoralis</u>	-	-	-	1.8	0.9	-	-	-	-	-
<u>C. caraboides</u>	-	-	-	0.6	-	-	-	-	-	-
<u>F. vulgaris</u>	-	-	-	-	-	0.3	-	-	-	-
<u>N. brevicollis</u>	0.1	0.1	0.2	1.0	0.5	0.3	0.8	0.6	0.1	0.03
<u>N. gyllenhali</u>	-	-	-	0.3	0.8	-	-	-	-	-
<u>C. micropterus</u>	-	-	0.1	-	1.1	0.1	0.1	-	-	-
<u>C. piceus</u>	-	0.1	0.3	0.4	0.3	0.1	-	-	-	-
<u>F. madida</u>	-	0.7	3.9	11.8	15.6	39.8	11.3	10.3	-	-
Total	0.1	0.9	4.5	15.9	20.5	41.7	12.2	10.9	0.1	0.0

TABLE 72

Theoretical numbers of predators in 1968/69 catch

	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Lower Hillside										
C. catenulatus	-	-	-	-	-	-	-	0.5	-	-
C. nemoralis	-	0.5	1.7	1.0	-	-	-	0.5	-	-
C. violaceus	-	-	0.8	-	-	0.7	-	-	-	-
F. vulgaris	-	0.2	-	0.9	-	-	-	-	-	-
N. brevicollis	0.05	0.04	0.05	0.6	0.5	0.03	0.05	0.08	0.06	0.02
C. fuscipes	-	-	-	0.4	-	-	-	0.8	-	-
C. melanocephalus	-	-	-	-	-	-	0.02	-	-	-
F. madida	0.8	1.6	2.4	3.9	5.9	4.0	1.6	1.3	0.3	-
Total	0.8	2.3	5.0	6.8	6.4	4.7	1.7	3.2	0.4	0.0

TABLE 73

Theoretical numbers of predators in 1968/69 catch

	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Field										
<u>C. nemoralis</u>	-	0.7	-	-	-	-	-	-	-	-
<u>C. caraboides</u>	-	-	-	0.7	-	0.7	-	-	-	-
<u>F. nigra</u>	-	-	-	-	4.5	8.4	-	-	-	-
<u>F. vulgaris</u>	-	-	-	-	0.5	1.3	-	0.3	-	-
<u>N. brevicollis</u>	-	0.02	0.01	2.3	0.3	0.04	0.9	0.9	0.1	0.03
									January	0.04
<u>F. madida</u>	-	-	-	0.2	0.8	4.3	0.2	0.2	-	-
Total	-	0.7	0.0	3.2	6.1	14.7	1.1	1.4	0.1	0.0

(D) Possible Future Studies

This study has shown that the larger carabid beetles can be predators of slugs, and that other invertebrates such as stapylinids, silphids and harvestmen are also involved in the relationship either as predators or scavengers. Now that some idea of the species involved has been obtained, and some of the methods which can be used to study the relationships have been developed, the next step would be to attempt to discover the importance of this predation in field populations of slugs.

The main difficulty would be determining the absolute numbers of slugs and predaceous invertebrates in different habitats. At present there seems to be no doubt that the best method of sampling slugs is by flotation from turf or soil samples which have been taken to the laboratory. This method is quite unsuitable for other more active invertebrates such as beetles, the majority of which would escape when the sample was being removed.

A mixture of methods with flotation for slugs and pitfall trapping for the others would also seem to be unsuitable because the removal of the turf etc. would destroy the habitat and it would not be possible to determine the numbers of slugs before and after predation. If sampling for slugs was carried out one day and trapping for predators the night before there would be no guarantee that all the slugs and predators counted would have been active at the same time. (The flotation method removes all the slugs not only those which have been active on the surface).

It would be possible by the use of bait and, to a lesser extent, boards to estimate the numbers of slugs in different areas, and by capture/recapture methods the number of predators in the same places, but such values would be approximate and would inevitably overlook microhabitat differences. General impressions could be gained that, for example, in one type of habitat the populations of slugs and beetles are both high, while in another there are proportionately more slugs, but it would be difficult to analyse such results or to derive any meaning from them.

Theoretically the balance between the populations of slugs and predators could be investigated by eliminating the predators in one particular area by the use of insecticides etc. (which would have to be non-molluscicidal) and observing the effects of this on the numbers of slugs. The area would have to be enclosed to prevent the immigration of other insects and the treatment would result in a highly artificial set of conditions, but it could give an indication of how the natural balance works.

As far as laboratory experiments are concerned the grass arena used by Stephenson (1964) is the nearest approximation to natural field conditions one can have. To use this with confidence one would have to overcome the problem of preventing slugs escaping while keeping the relative humidity and temperature as natural as possible. (Covering cultures with lids undoubtedly affects these). Also one would have to obtain from field studies some idea of the area each slug and predator should occupy so that their relationship in space was normal, without unnatural overcrowding.

The main difficulty in laboratory experiments is the problem of the predators' food preferences. With the exception of <u>Cychrus caraboides</u> and possibly Phosphuga atrata no invertebrates, in the area under study, fed exclusively on slugs. Under field conditions no circumstances could arise in which alternative food would not be available, and one would have to make allowances for this if one wished to apply any findings derived from laboratory work to the situation in the field.

In conclusion, there is little doubt that further research into the association between slugs and their predators, vertebrate and invertebrate, would be interesting, and being a part of biological control studies, scientifically rewarding. Such research would ideally be made by a team of workers, with a division of duties between field work and laboratory studies. In this way a large volume of data, derived from many different habitats, could be amassed and analysed, and, hopefully, this would shed more light on the intricate relationships which exist between slugs and their predators.

ACKNOWLEDGMENTS

I wish to thank Dr. W. J. Guild for supervising this work, Dr. T. W. Tinsley for giving an outline of serological methods which could be used, and Mr. J. K. Miller, M.V.Sc., M.R.C.V.S. for developing this, preparing the antiserum and giving advice on the techniques which were used in the serological tests.

REFERENCES

BAILEY, N. T. J. (1959). Statistical methods in biology. 200 pp. London. English University Press.

BOYD, J. MORTON (1960). Studies of the differences between the fauna of grazed and ungrazed grassland in Tiree, Argyll. Proc. zool. Soc. Lond. 135, 33 - 54.

BRIGGS, J. B. (1957). Some experiments on control of ground beetles damage to strawberries. Rep. E. Malling Res. Stn. 1956, 142 - 145.

_____ (1961). A comparison of pitfall trapping and soil sampling in assessing populations of two species of ground beetles(Col.:Carabidae) Rep. E. Mall. Res. Stn. 1960, 108 - 112.

BROOKE, M. M. & PROSKE, H. O. (1946). Precipitin test for determining natural insect predators of immature mosquitoes. J. natn. Malar. Soc. 5. 45 - 56.

CHAUVIN, R. (1967). The world of the insect. 154. London. Weidenfeld & Nicolson.

CROWLE, A. J. (1961). Immunodiffusion. 333 pp. New York and London. Academic Press.

DANTHANARAYANA, W. (1969). Population dynamics of the weevil Sitona regensteinsis (Hbst.) on broom. J. Anim. Ecol. 38, 1 - 18.

DAVIES, M. J. (1953). The contents of the crops of some British carabid beetles. Entomologist's mon. Mag. LXXXIX, 18 - 23.

DAVIES, M. J. (1959). A contribution to the ecology of species of Notiophilus and allied genera. (Col., Carabidae). Entomologist's mon. Mag. 95, 25 - 28.

DAWSON, N. (1965). A comparative study of the ecology of eight species of fenland Carabidae (Coleoptera). J. Anim. Ecol. 34, 299 - 314.

DEMPSTER, J. P., RICHARDS, O. W. & WALOFF, N. (1959). Carabidae as predators on the pupal stage of the Chrysomelid beetle Phytodecta olivacea (Forster). Oikos 10, 65 - 70.

DRIFT, J. VAN DER. (1951). Analysis of the animal community in a beech forest floor. Tijdschr. Ent. 94 : 1 - 168. Cited by Greenslade, P.J.M. in Trans. Soc. Brit. Ent. (1965) 16, 149 - 179.

EMDEN, F. I. VAN (1942). A key to the genera of larval Carabidae (Col.). Trans. R. ent. Soc. London 92, 1 - 99.

FOWLER, W. W. (1887). The Coleoptera of the British Islands I 269 pp. London. Lowell Reeve.

_____ (1888). The Coleoptera of The British Islands II 444 pp. London. Lowell Reeve.

FOWLER, W. W. & DONISTHORPE, H. ST. J. (1913). The Coleoptera of the British Islands VI supplement. 201. London. Lowell Reeve.

FOX, C. J. S. & MACLELLAN, C. R. (1956). Some Carabidae and Staphylinidae shown to feed on a wireworm Agnotes sputator (L.) by the precipitin test. Can. Ent. 88, 228 - 231.

GLENDENNING, R. (1952). Slug control in Canada. Canada Dept. Agric. Entomology Processed Publ. Series No. 85, 1 - 5.

GREENSLADE, P. J. M. (1964). Pitfall trapping as a method for studying populations of Carabidae. J. Anim. Ecol. 33, 301 - 310.

______ (1965). On the ecology of some British carabid beetles with special reference to life histories. Trans. Soc. Brit. Ent. 16, 149 - 179.

HIKIMIUK, A. I. (1948). (A quantitative study of seasonal phenomena in the life of Carabus species) (In Russian). Bull. Soc. Nat. Moscow 1153. 4 - 13. Cited by Greenslade, P. J. M. in Trans. Soc. Brit. Ent. (1965), 16, 149 - 179.

HUNTER, P. J. (1969). An estimate of the extent of slug damage to wheat and potatoes in England and Wales. N.A.A.S. q. Rev. No. 85. 31 - 36.

HUSSEY, N. W. & LANE, J. (1956). Necrophagous coleoptera trapped in different habitats in Midlothian. Entomologist's mon. Mag. XCII, 201 - 206.

JOY, N. H. (1932). A practical handbook of British beetles I 622 pp. II 194 pp. London. H. F. and G. Witherby.

KABACICK, D. (1957). Z badan nad biegaczowatymi (Carabidae) lasu sosnowego. Ecol. Polska B. 3 239 - 242. Cited by Greenslade, P.J.M. in J. Anim. Ecol. 1964, 33, 301 - 310.

KAUFMANN, R. R. U. (1937). Investigations on beetles associated with carrion in Pannal Ash, near Harrogate. II. Entomologist's mon. Mag. LXXIII, 227 - 233.

KEVAN, D. K. (1945). The Coleoptera of an Edinburgh garden. Entomologist's mon. Mag. LXXXI, 112 - 113.

KIRCHNER, H. (1960). Untersuchungen zur Okologie feld bewohnender Carabiden. Dissertation, University of Cologne. Cited by Greenslade, P.J.M. in Trans. Soc. Brit. Ent. (1965), 16, 149 - 179.

KRUMBIEGEL, I. (1932). Untersuchungen uber physiologische Rassenbildung. Zool. Jb., 63, 182 - 280. Cited by Greenslade, P. J. M. in Trans. Soc. Brit. Ent. (1965), 16, 149 - 179.

LARSSON, S. G. (1939). Entwicklungstypen und Entwicklungszeiten der danischen Carabiden. Ent. Medd. 10, 277 - 560. Cited by Greenslade,P.J.M. in Trans. Soc. Brit. Ent. (1965), 16, 149 - 179.

LINDROTH, C. H. (1945-49). Die Fennoskandischen Carabiden. 3 vols. Goteborg. Cited by Greenslade, P. J. M. in Trans. Soc. Brit. Ent. (1965), 16, 149 - 179.

LINSSEN, E. F. (1959). Beetles of the British Isles. First series. 172 - 173. London. Frederick Warne.

LUFF, M. L. (1969). The larvae of the British Carabidae (Coleoptera). I. Carabini and Cychrini. Entomologist 102, No. 1278, 245 - 263.

MITCHELL, B. (1963). Ecology of two carabid beetles, Bembidion lampros (Herbst) and Trechus quadristriatus (Schrank). II Studies on populations of adults in the field, with special reference to the technique of pitfall trapping. J. Anim. Ecol. 32, 377 - 392.

PENNEY, M. M. (1966). Studies on certain aspects of the ecology of Nebria brevicollis (F.) (Coleoptera, Carabidae). J. Anim. Ecol. 35, 505 - 512.

_____ (1969). Diapause and reproduction in Nebria brevicollis (F.) (Coleoptera: Carabidae). J. Anim. Ecol. 38, 219 - 235.

POLLARD, E. (1968a). Hedges. III The effect of removal of the bottom flora of a hawthorn hedgerow on the Carabidae of the hedge bottom. J. appl. Ecol. 5, 125 - 139.

______ (1968b). Hedges. IV A Comparison between the Carabidae of a hedge and field site and those of a woodland glade. J. appl. Ecol. 5, 649 - 657.

RITCHER, P. O. (1958). Biology of Scarabaeidae. A. Rev. Ent. 3. 311 - 334.

SCHERNEY, F. (1960). Beitrage zur Biologie und okonomischen Bedeutung rauberisch lebender Käferarten. Z. ang Ent. Bd. 47, 231 - 255.

STEPHENSON, J. W. (1964). Rothamstead a. Rep. 1964. 188.

______ & KNUTSON, L. V. (1966). A resumé of recent studies of invertebrates associated with slugs. J. econ. Ent. 59, 356 - 360.

TAYLOR, J. W. (1900). A monograph of the land and freshwater Mollusca of the British Isles. Structural and general volume. Part VII, 419 - 420.

TIPTON, J. D. (1960). Some aspects of the biology of the beetles Nebria brevicollis (F.) and Feronia caerulescens (L.). Ph.D. Thesis. University of Reading. Cited by Greenslade, P. J. M. in Trans. Soc. Brit. Ent. (1965), 16, 149 - 179.

VOGEL, R. (1915). Beitrag zur Kenntnis des Baues und der Lebensweise der Larve von Lampyris noctiluca. Z. wiss. Zool. 112, 291 - 432.

WILLIAMS, G. (1959a). The seasonal and diurnal activity of the fauna sampled by pitfall traps in different habitats. J. Anim. Ecol. 28, 1 - 13.

_____ (1959b). Seasonal and diurnal activity of Carabidae, with particular reference to *Nebria*, *Notiophilus* and *Feronia*. J. Anim. Ecol. 28, 309 - 330.